Fishery Bulletin

Vol. 80, No. 3 July 1982

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Seattle, Washington

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Fishery Bulletin

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DEVELOPMENT OF EGGS AND LARVAE OF THE WHITE CROAKER, *GENYONEMUS LINEATUS* AYRES (PISCES: SCIAENIDAE), OFF THE SOUTHERN CALIFORNIA COAST

WILLIAM WATSON[1]

ABSTRACT

Eggs and larvae of the white croaker, *Genyonemus lineatus*, were collected near the San Onofre Nuclear Generating Station in 1978 and 1979. A developmental series based on 59 eggs and 168 larvae and early juveniles was assembled.

Live *G. lineatus* eggs are pelagic, transparent, and spherical, averaging 0.85 mm in diameter with a single oil droplet of 0.23 mm. Preserved, newly hatched larvae average 1.57 mm SL and are not well developed. Larval development is a gradual process. Notochord flexion begins at ca. 5.4 mm SL and is complete by ca. 6.4 mm SL. Dorsal and anal fin anlagen appear at ca. 5 mm SL and the full complement of rays is present in each fin by ca. 8.2 mm SL. Pelvic differentiation begins at ca. 5.3 mm SL and is finished by ca. 8.6 mm SL. Pectoral rays begin to develop at ca. 7.8 mm SL and all are present by ca. 13 mm SL.

Larval pigmentation is largely restricted to the dorsum at hatching, but migrates to the ventral midline during early development. Melanophores are restricted to the ventrum and gut through much of the subsequent larval period. A barred pattern develops during transition to the juvenile stage.

Genyonemus lineatus larvae are distinguishable from similar cooccurring species by the presence of a nape melanophore and larger melanophores in the midventral trunk series at myomeres 9-10 and 16-18.

The sciaenid genus, *Genyonemus*, is represented by a single species, *G. lineatus* (Ayres), the white croaker. It occurs along the west coast of North America from central Baja California to southern British Columbia (Miller and Lea 1972), although its numbers are reduced north of San Francisco, Calif. (Frey 1971). In southern California the white croaker is a common inshore species of modest sport and commercial value (Skogsberg 1939; Frey 1971). Its larvae rank second in abundance only to those of the northern anchovy, *Engraulis mordax*, among the inshore ichthyoplankters off San Onofre, Calif. (Walker et al. 1980[2]).

Despite its abundance in southern California, the early life history of *G. lineatus* is poorly known. Seasonal spawning cycles are described based on gonadal studies (Goldberg 1976), and the duration of the egg stage is mentioned by Morris (1956), who reared *G. lineatus* from field-collected eggs through 19-d-old larvae. Larvae are not described, although Morris (1956) gives dimensions of the egg.

Beginning in January 1978, Marine Ecological Consultants of Southern California initiated a study of the inshore ichthyoplankton off San Onofre (Fig. 1) for the Marine Review Committee of the California Coastal Commission (Barnett and Sertic 1979[3]). During this study approximately 48,000 *G. lineatus* larvae were sorted from the samples, providing an opportunity to construct a developmental series through the early juvenile stage. Live plankton samples provided eggs for rearing purposes. This paper describes the egg and larval development of *G. lineatus* as determined from these series.

MATERIALS AND METHODS

Egg and larval descriptions are based on detailed observation of 59 eggs, 29 reared larvae,

[1]Marine Ecological Consultants, 533 Stevens Avenue, Solana Beach, CA 92075.

[2]Walker, H. J., A. M. Barnett, and P. D. Sertic. 1980. Seasonal patterns and abundance of larval fishes in the nearshore Southern California Bight off San Onofre, California. Marine Ecological Consultants of Southern California, 533 Stevens Ave., Solana Beach, CA 92075, 16 p.

[3]Barnett, A. M., and P. D. Sertic. 1979. Preliminary report of patterns of abundance of ichthyoplankton off San Onofre and their relationship to the cooling operations of SONGS. Marine Review Committee Document 79-01, p. 1-1 to 4-5. Marine Review Committee of the California Coastal Commission, San Francisco, Calif.

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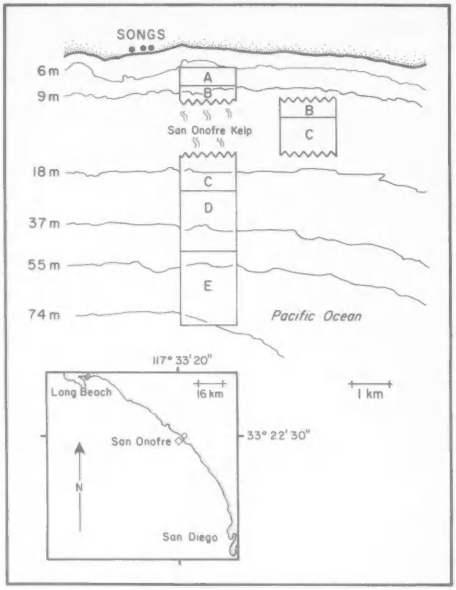

FIGURE 1.—Chart of the sampling area and its position off the southern California coast. SONGS = San Onofre Nuclear Generating Station.

and 139 field larvae. These were collected in 1978 and 1979 between the 6 and 20 m isobaths near the San Onofre Nuclear Generating Station (Fig. 1; Barnett and Sertic footnote 3).

Eggs used only for egg description were maintained at ambient air temperature (ca. 20°C) while those reared for larval description were maintained near their collection temperatures (13.4°-14.3°C). The sequence of developmental events in reared specimens was confirmed by comparison with field specimens.

Plankton samples were preserved in the field in 5% seawater-Formalin[4] and specimens later sorted in the laboratory. These were stored in 2.5-5% seawater-Formalin. Reared specimens were preserved in 2.5% seawater-Formalin.

Because reared *Genyonemus* larvae often are more heavily pigmented than field specimens, the latter were used as the principal descriptive source. Yolk-sac larvae were primarily reared specimens, owing to the difficulty of obtaining undamaged field specimens of this size. Twenty field specimens from the early larval stage through transition to the juvenile were cleared and stained with alizarin following the method of Hollister (1934) to determine the sequence of skeletal ossification.

Measurements were made to the nearest 0.03 mm at 25× using a binocular dissecting microscope equipped with an ocular micrometer. Drawings were made with the aid of a camera lucida. Pigmentation illustrated for yolk-sac larvae represents fresh material; the pattern is largely lost after several weeks of preservation.

Developmental stages follow the terminology of Ahlstrom and Ball (1954), except that the transitional period between the larval and juvenile stages is considered to begin when the first scales appear and to end when scalation is essentially complete. All fin rays and myomeres (preanal plus postanal) were counted on each specimen, when distinguishable. Dimensions measured were body depth, eye diameter, head length, preanal length, preanal fin length, snout length, and standard length. These dimensions are defined in the literature (e.g., Saksena and Richards 1975; Powles 1980).

EMBRYONIC DEVELOPMENT

The *G. lineatus* egg is pelagic, spherical or nearly so, and transparent, with an unsculptured chorion and unsegmented yolk (Fig. 2). It usually contains a single colorless to slightly yellowish oil droplet, although in the early stage it may contain two or three oil droplets which later coalesce. Thirty-eight live eggs collected from the plankton averaged 0.85 mm (SD = 0.02 mm) in diameter, with a single oil droplet of 0.23 mm (SD = 0.02 mm). The perivitelline space was very small (<0.04 mm). These dimensions are similar to those given by Morris (1956) for *G. lineatus* eggs collected from the plankton: egg diameter 0.9 mm and oil droplet diameter 0.2 mm. Twenty-one eggs preserved for 111 d in 2.5% seawater-Formalin were slightly oval, averaging 0.84 by 0.83 mm (SD = 0.02 mm) in diameter, with a single oil droplet of 0.21 mm (SD = 0.01 mm) and a perivitelline space of 0.05 mm (SD = 0.02 mm).

The embryo is unpigmented through gastrulation (Fig. 2a, b). During eye capsule formation the first few small melanophores appear on the distal side of the oil droplet and on the yolk adjacent to the oil droplet (Fig. 2c). Midlateral, middorsal, and a few scattered dorsolateral trunk

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

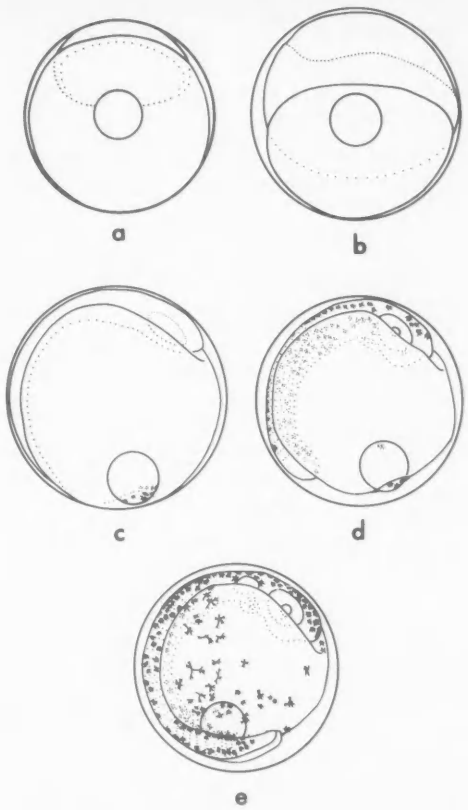

FIGURE 2.—Development of the *Genyonemus lineatus* egg: a) blastula stage, 0.78 mm diameter; b) gastrula stage, 0.86 mm diameter; c) early embryo just prior to blastopore closure, 0.90 mm diameter; d) tail bud stage, 0.84 mm diameter; e) late stage, 0.84 mm diameter. All illustrations are of live eggs. Note that oil droplets are somewhat smaller than average in this group of eggs.

melanophores appear shortly thereafter. About 5 h after eye capsule formation (at 20°C) small melanophores surround the trunk and are scattered dorsally on the head (Fig. 2d). A few melanophores occur on the yolk adjacent to the tail bud at this stage. As development continues the dorsal head pigmentation increases and trunk melanophores become situated primarily dorsally and dorsolaterally. Yolk melanophores increase in number until they nearly surround the yolk just before hatching (Fig. 2e).

The oil droplet is located opposite or adjacent to the embryo through gastrulation (Fig. 2a, b). During the latter part of the egg stage the tail of the developing embryo grows past the oil droplet, which ultimately is situated adjacent to the embryo just anterior to the anus (Fig. 2e).

Optic capsules develop almost simultaneously with blastopore closure and just prior to somite development. Lens development begins at about the four myotome stage.

Somite differentiation begins just behind the head and continues posteriorly. Kuppfer's vesicle first becomes apparent near the tip of the tail bud at about the 4 somite stage and persists to the 18 somite stage. Heart and finfold development are initiated at about the 18 somite stage and the tail first separates from the yolk shortly thereafter. By the end of the egg stage the embryo has 25-26 myomeres, otic capsules with at least the sagittae developing, a simple tubular gut, wide finfold, and functional heart.

Preserved eggs collected from the plankton at 1900 PST on 29 January 1979 were largely in the two, four, and eight cell stages. Live eggs from the same sample began gastrulation after 20-22 h of incubation (ca. 20°C) and eye capsules developed at about 26-28 h. The 18 somite stage was reached at about 38-40 h and the full somite complement attained by 43-45 h. All larvae had hatched by 52 h.

YOLK-SAC LARVAE

Pigmentation

The pigmentation of newly hatched larvae closely resembles that of late stage eggs, with melanophores concentrated primarily dorsally and dorsolaterally on the head and trunk (Fig. 3a). Additional pigment includes a characteristic large dendritic melanophore extending upward from the nape to the margin of the finfold, a large midventral melanophore about halfway between the anus and tip of the tail (one or two small lateral melanophores may occur here as well), and one to three small middorsal and midventral melanophores near the tip of the notochord. One or two melanophores usually occur ventrally on the gut, near the anus. Oil droplet pigmentation is mainly proximal. A few melanophores are usually scattered on the yolk sac. The nape, oil droplet and gut, and midtail pigment appears as three distinct bands in live larvae. Only the nape and midtail melanophores may be expected to survive prolonged Formalin preservation.

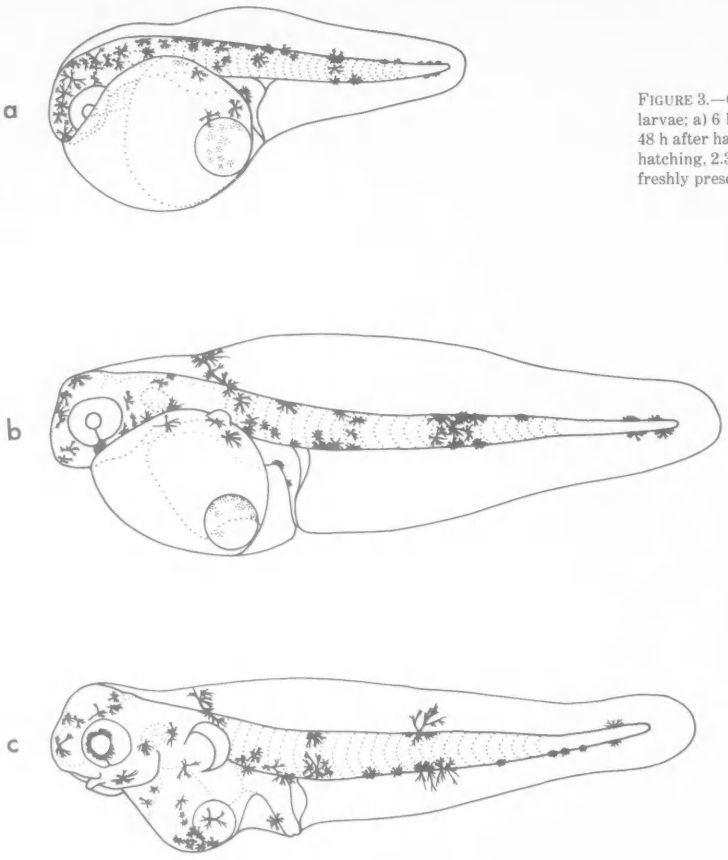

FIGURE 3.—*Genyonemus lineatus* yolk-sac larvae: a) 6 h after hatching, 1.54 mm; b) 48 h after hatching, 2.48 mm; c) 68 h after hatching, 2.36 mm. All illustrations are of freshly preserved reared larvae.

Head pigment changes little during the first 60 h (ca. 13°C). After this it condenses to a few melanophores over the forebrain and midbrain. These melanophores may be lost by the end of the yolk-sac stage except for one or two melanophores on the otic capsule. A small melanophore first appears at the angular bone just at the end of the yolk-sac stage. Eye pigmentation begins at about 60 h (Fig. 3c) and is complete by 120 h after hatching (ca. 13°C).

During the first 24 h after hatching the dorsal trunk melanophores begin to migrate ventrally, condensing into bands at the nape, the anus, and midtail at myomeres 16-18 (Fig. 3b). This pattern persists but becomes indistinct as melanophores continue to migrate ventrally.

By the end of the yolk-sac stage dorsal trunk pigment consists only of the large nape-finfold melanophore, one or two smaller melanophores near the level of the anus, one in the region of myomeres 16-18, and one or two near the tip of the notochord. Lateral melanophores may persist in these same areas, although more often they do not. Midventral trunk pigment increases to a series of 8-10 melanophores, with those at myomeres 9-10 and 16-18 usually larger.

Oil droplet and yolk-sac pigment changes only by condensing as the yolk is consumed. The ventral hindgut melanophores persist through the yolk-sac stage with the lower migrating to a position adjacent to the anus. A single small melanophore usually moves to the dorsal midline of the hindgut where the hindgut turns downward at the fifth or sixth myomere. After about 60 h one

or two melanophores may overlie the gut at the level of the soon-to-inflate swim bladder at myomeres 1 and 2.

Morphology

Genyonemus lineatus larvae hatch in a relatively undifferentiated state with unpigmented eyes, otic capsules usually with sagittae, a functional but simple tubular heart, straight tubular gut, large yolk sac, and posterior oil droplet. No mouth, branchial apparatus, or other viscera are apparent.

Pectoral buds appear during the second day after hatching and pectoral membranes are present on the third. The mouth opens and the operculum becomes discernible during the third day. Gut differentiation begins at this time. Yolk exhaustion and swim bladder inflation occur on the sixth day. Feeding, and consequently the end of the yolk-sac stage, is initiated during the sixth or seventh day after hatching (at ca. 13°-14°C).

Larvae lengthen during the yolk-sac stage, from a preserved hatching length of 1.57 mm ($n = 4$, SD = 0.02 mm) to 2.41 mm ($n = 4$, SD = 0.02 mm) at yolk exhaustion. Yolk-sac length declines from 0.86 mm ($n = 4$, SD = 0.04 mm) at hatching to zero. Head length, preanal length, and eye diameter change little during the yolk-sac stage.

LARVAE

Pigmentation

Genyonemus lineatus larvae are quite variable in degree of pigmentation (e.g., midwinter larvae often are more lightly pigmented than spring larvae), although the basic pattern is conservative. Because of this variability, pigmentation is described more fully than might otherwise be warranted. Illustrations are of typical (i.e., late winter) specimens.

The head typically is moderately pigmented at the beginning of the larval stage (Fig. 4a). Single small melanophores are nearly always present on the snout and at the angular bone, as many as four or five may be scattered over the fore- and midbrain regions, and one or two are often located in the floor of the otic capsule. Some specimens have an elongate melanophore laterally on the mandible.

The snout melanophore is lost soon after yolk absorption and the snout remains unpigmented throughout larval development. Small melanophores begin to appear between the nostrils at ca. 17 mm and rapidly proliferate to form a band which persists until becoming obscured by the increasing head pigmentation in the juvenile stage.

The melanophore at the angular bone persists through the juvenile stage. Mandibular pigment typically is absent until the beginning of transition at ca. 13 mm, when a pair of melanophores appears at the center of the mandible. The number increases to six or eight by the beginning of the juvenile stage (ca. 17 mm). Premaxillary pigmentation begins shortly before transition, with a pair of melanophores at the center of the upper jaw. Four to six more melanophores are added by the beginning of the juvenile stage. Some small specimens may have one or two melanophores in the central gular region. These rarely persist beyond ca. 5 mm.

Pigment on top of the head declines rapidly early in the larval stage, and is absent after ca. 2.8 mm. During the transitional period melanophores again appear on the head, beginning with a pair over the midbrain region at ca. 14.8 mm. Melanophores rapidly proliferate to form bands over the midbrain by the beginning of the juvenile stage.

Opercular pigmentation is acquired just before the juvenile stage, with a pair of melanophores under the central opercular region. One or two external melanophores develop on the upper operculum at ca. 17.2 mm and quickly increase in number to form a dark patch.

Otic floor pigment is most often present in larvae <4 mm and absent in larger specimens. At ca. 9.5 mm a melanophore appears under the anterior hindbrain, followed by an anterolateral melanophore on each side at ca. 10 mm. A second ventrolateral melanophore is acquired here during transition (ca. 13 mm) and by the beginning of the juvenile stage the anterior hindbrain is usually surrounded by a heavy pigment band.

At the beginning of the larval stage dorsal trunk pigment includes one or two nape-finfold melanophores, usually a single middorsal melanophore between myomeres 16 and 18, often a middorsal or dorsolateral melanophore between myomeres 6 and 8, and occasionally one or two small middorsal melanophores near the tip of the notochord (Fig. 4a). Lateral trunk pigment which persists into the larval stage is located at myomeres 6-8 and 16-18. This usually is lost by 2.8 mm although an occasional specimen of any

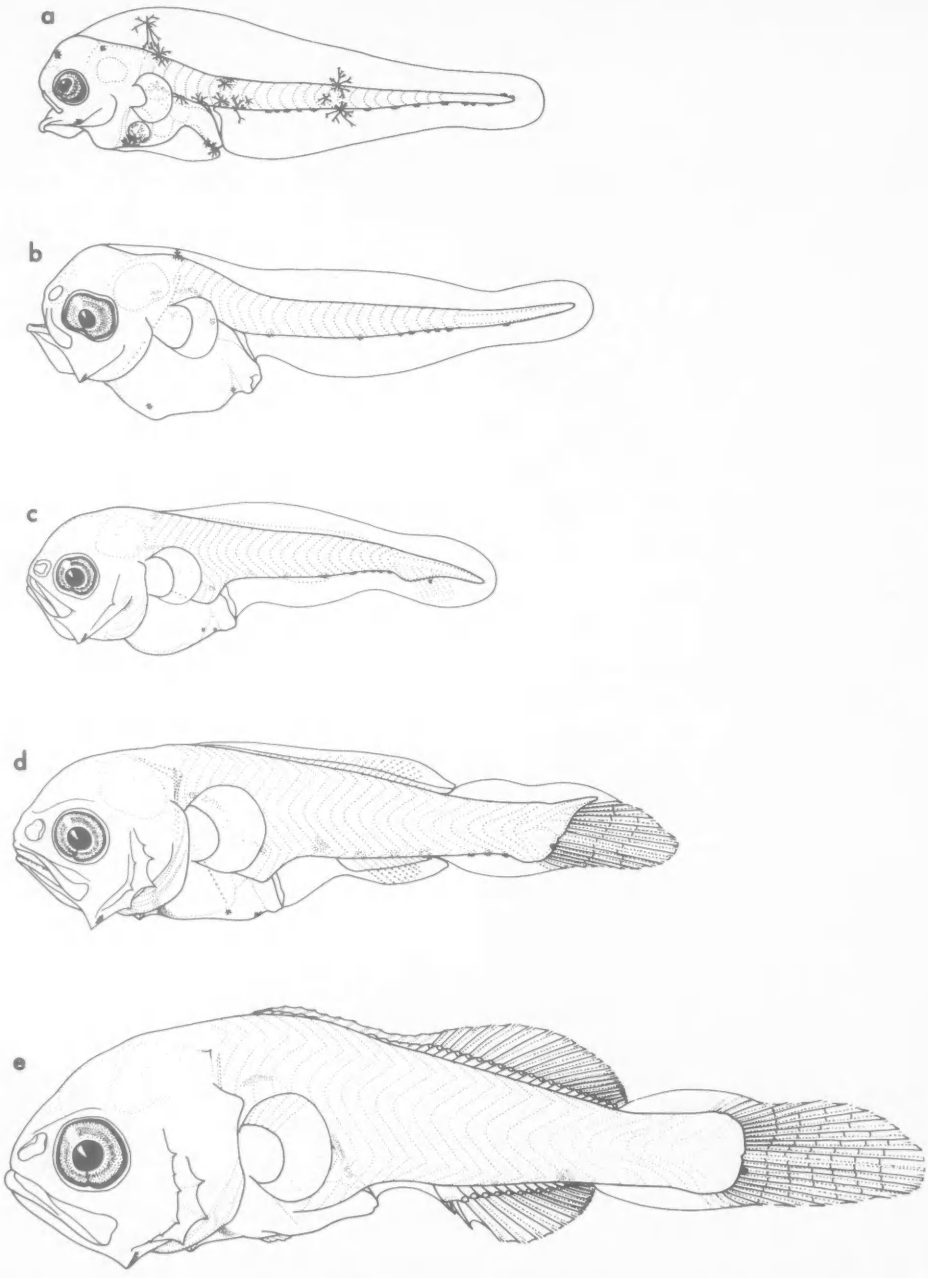

FIGURE 4.—*Genyonemus lineatus* larvae: a) 2.73 mm; b) 3.04 mm; c) 5.15 mm; d) 6.18 mm; e) 8.16 mm. All illustrations are of field specimens.

size may retain a midlateral melanophore in the myomere 16-18 region. The ventral midline melanophore series increases quickly from 8 to 10 late in the yolk-sac stage to 15-21 by ca. 2.6 mm. The melanophores at myomeres 9-10 and 16-18 remain largest.

The dorsal notochord tip melanophores and those at myomeres 6-8 are lost by ca. 2.8 mm (Fig. 4b). The melanophore at myomeres 16-18 often persists to 5 mm, and may continue until 6 mm in some specimens. The nape melanophore migrates internally and is obscured by the overlying tissue as early as ca. 2.5 mm or as late as ca. 6.1 mm, but most often between 4.8 and 5.6 mm. Following the internal migration of the nape melanophore the trunk remains unpigmented dorsally and laterally through the larval and transitional periods. Early in the juvenile stage a barred pattern develops (Fig. 5). At 17.2 mm a short bar crosses the nape and may extend laterally to the level of the supracleithral spine. A second bar extends to the midlateral line from dorsal spines VII-X, a third and fourth from dorsal rays 5-10 and 16-21, and a fifth crosses the peduncle. Six to nine bars ultimately develop in the juvenile stage, counting the snout and cranial bars. Trunk melanophores in these bars are principally myoseptal.

The midventral trunk melanophores number between 15 and 21 at the beginning of the larval stage. They begin coalescing immediately, but from 7 to 19 remain through 4.5 mm. By the beginning of caudal flexion (ca. 5.5 mm) they decline to between 2 and 12, and thereafter number between 2 and 6. The melanophore between myomeres 16 and 18 is always largest and persists through the larval stage (Fig. 4e). This melanophore lies at the posterior end of the anal fin in older larvae. The second largest midventral melanophore, which initially lies between myomeres 9 and 10, shifts one to three myomeres posteriorly and migrates internally by the time of anal fin anlage formation (Fig. 4c, d). It often persists through the larval stage, lying near the anal fin origin in older specimens. One to three small melanophores may also remain in the ventral midline between myomeres 20 and 25 through the larval period. One small melanophore usually persists near the end of the notochord, becoming located at the central distal margin of the developing hypural complex during flexion. As the caudal fin rays ossify, one to a few melanophores develop along the central and lower fin ray bases. During transition internal melanophores begin to appear along the urostyle and lower hypurals, and a band of pigment develops along the distal one-third of the caudal rays.

Soon after anal fin completion melanophores develop at the anal fin ray bases. These occur first on either side between anal soft rays 1 and 4, and proceed both anteriorly and posteriorly. The number of melanophores is variable—usually three or fewer in larvae <9 mm and five or fewer in larger specimens.

The gut region is moderately pigmented at the beginning of the larval period: a single external melanophore normally lies on each side just behind the upper pectoral insertion; one to three pairs of melanophores occur on top of the swim

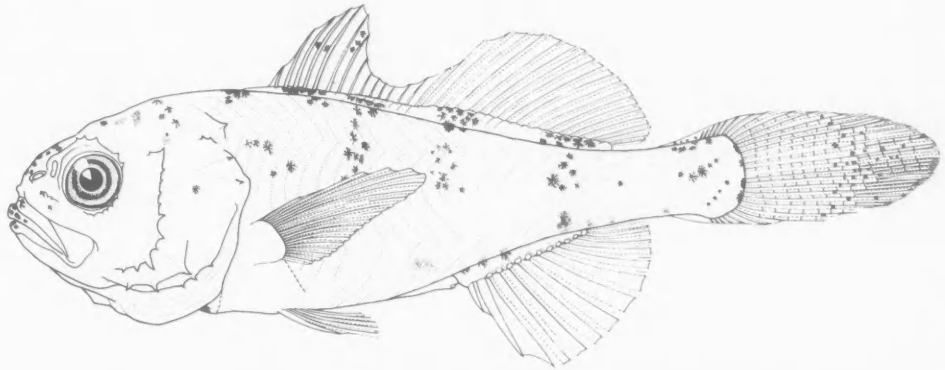

FIGURE 5.—*Genyonemus lineatus* early juvenile, 19.20 mm.

bladder; as many as two lie on the middorsal surface on the gut just behind the swim bladder; one small melanophore usually lies on the dorsal hindgut just where it turns downward at myomere 5 or 6; a larger melanophore lies adjacent to the hindgut just anterior to the anus, one rather large melanophore may lie on the anterior midline of the visceral mass just below the level of mideye; none to several small melanophores are scattered ventrally and ventrolaterally over the anterior gut.

Gut pigment generally decreases during larval development. The melanophore behind the pectoral base rarely persists beyond 5.2 mm. Swim bladder pigment increases but remains restricted to its dorsal surface through the larval period. All other dorsal gut pigment except the melanophore on the hindgut is lost by ca. 3 mm and usually does not reappear until ca. 11.2 mm, near the end of the larval stage. The dorsal melanophore on the hindgut is present more often than not (present in 63% of the larvae examined) and is nearly always quite small in specimens smaller than ca. 8 mm. In larger specimens it is nearly always present (in 95% of the larvae examined) and increases in size (occasionally others are added as well) to nearly cover the dorsal surface on the hindgut by ca. 11.2 mm (Fig. 5). In older specimens melanophores begin to fill in between the swim bladder and hindgut, so that in early juveniles the dorsal gut cavity is often entirely pigmented.

The melanophore just anterior to the anus usually persists through ca. 6 mm but is rarely present in larger specimens. Other ventral gut pigment is quite variable early in the larval period, ranging from one to several melanophores typically on the anterior half of the gut. The ventral midline of the gut often remains unpigmented throughout larval life. Only a single melanophore just anterior to the cleithral symphysis commonly remains after 5 mm (present in 64% of the larvae examined). During the transitional period one or two additional melanophores develop to form a series along the midline of the isthmus. After completion of the pelvic fin (ca. 9 mm) a single melanophore may appear between the pelvic bases. During transition a ventral midline series of two or three melanophores may arise behind the pelvic fin bases.

The large internal melanophore located anteriorly on the upper visceral mass migrates ventrally as larval development proceeds: when present it is nearly always on the upper visceral mass in larvae smaller than ca. 4 mm, is most frequently located halfway down between 4 and 6 mm (Fig. 4c), and is nearly always present at the lower anterior margin of the visceral mass in specimens larger than ca. 6 mm (Fig. 4d).

Fin Development

At the beginning of the larval period *G. lineatus* larvae have only a broad medial finfold and pectoral fin without rays. Subsequent fin development follows a typical sciaenid sequence (e.g., Powles 1980; Pearson 1929).

The caudal fin is first to develop. The caudal anlage appears at ca. 3.8 mm and the central four to six principal rays begin to ossify at ca. 4.8 mm. Notochord flexion begins at ca. 5.4 mm and is complete at ca. 6.4 mm. The full complement of 9+8 principal caudal rays is ossified by the end of flexion. Further development includes the addition of secondary caudal rays (15 to 17 total by the early juvenile stage), branching of the central principal rays and lengthening of the fin. The central rays are longest throughout larval development.

Anal and dorsal fin anlagen appear nearly simultaneously at ca. 5 mm. The anal fin anlage is short, usually extending between myomeres 13 and 18. Differentiation begins with the most anterior anal soft ray bases just after the anlage first appears, and proceeds posteriorly. The sequence of anal fin ray differentiation follows that of the ray bases, beginning with the first soft ray at ca. 6 mm and proceeding posteriorly. All anal soft rays are discernible by ca. 6.7 mm, at which time the second anal spine begins to ossify. The first anal spine completes the anal fin ray complement at ca. 7.2 mm. Subsequent larval development consists of lengthening of the rays and ossification of the pterygiophores.

The dorsal anlage initially lies between the tenth and fifteenth myomeres and lengthens to myomeres 3-21 by ca. 6 mm. As in anal fin development, the anterior soft ray bases differentiate first, beginning at ca. 5.4 mm, and the soft rays ossify from the first ray posteriorly beginning at ca. 6 mm. The posterior 8 to 10 bases are undifferentiated as the first soft rays begin ossifying. Dorsal spine bases begin differentiating anteriorly at ca. 6.4 mm and the anterior spines appear at ca. 7.2 mm, about the time of acquisition of the full complement of dorsal soft rays. The dorsal spines ossify posteriorly, reaching the adult complement of 12 to 15 by 8.0-8.5 mm. The

dorsal fin is continuous, with the first dorsal much lower than the second initially. As growth continues the anterior spines (except the first) lengthen faster than the others, so that the dorsal fin is deeply notched by the beginning of the transitional period.

Pelvic fin buds first appear between 5.3 and 5.9 mm and the first one or two elements become visible at ca. 7.2 mm. Differentiation of rays proceeds toward the midline. The full complement of one small spine and five rays usually is attained by ca. 8.6 mm.

Pectoral rays first develop at ca. 7.8 mm, beginning from the upper pectoral base and proceeding downward. Five to nine upper rays are present by ca. 8.6 mm and the full complement of one small spine plus 17 to 18 rays is attained by ca. 12.7 mm, just before the transition to the juvenile stage. The upper pectoral rays lengthen much more than the lower rays as the fin grows, changing its outline from rounded to bluntly pointed.

Head Spination

Genyonemus lineatus acquires a number of small spines on the head during larval development. First among these is the spine at the angle of the preopercle at ca. 3.5 mm. A second spine is added just above the angle and a second row of preopercular spines begins developing at ca. 4.5 mm. Preopercular spination subsequently increases to between five and eight short spines in each row by the end of the larval period. Early juveniles may have as many as 12 spines in each row. An interopercular spine develops at ca. 5.5 mm. Interopercular spines vary in number between one and four throughout larval development. A subopercular spine develops at ca. 10.5 mm; as many as two or three may be present at the beginning of the juvenile stage. An opercular spine first appears at ca. 10.5 mm and remains throughout subsequent development.

A minute supracleithral spine emerges at ca. 6.6 mm. Up to three additional supracleithral spines may develop during the transition to juvenile.

The first supraocular spine becomes apparent at ca. 7.2 mm and is joined by an additional one or two spines by ca. 9.2 mm. As many as eight small supraocular spines may be present by the end of the transitional period.

Ossification

Initial skeletal ossification in *G. lineatus* begins with the cleithra. This is soon followed by the jaws and associated bones, some of the branchiostegals, opercular apparatus, and branchial apparatus, and the posterior skull. Premaxillary teeth appear next, followed by the first pharyngeal teeth. Dentary teeth arise later, about the beginning of vertebral and principal caudal fin ray ossification. Initiation of dorsal and anal soft fin ray and hypural ossification follows (Table 1). Anal fin spines precede the dorsal fin spines, which are followed by pelvic and then pectoral fin rays. All fin rays begin to ossify before their respective supporting structures. Somewhat more detailed descriptions of ossification follow.

In the smallest larva cleared (2.6 mm) the only stained structures are the cleithra and basioccipital. By ca. 4 mm the posterior parasphenotic has begun to ossify; parasphenotic ossification is complete and the exoccipitals begin to ossify at ca. 4.6 mm. Exoccipital ossification is essentially complete and posttemporal ossification is beginning at ca. 5.1 mm. Ossification of the frontal bones initiates at ca. 5.6 mm. The lacrimal ap-

TABLE 1.—Meristics of cleared and stained *Genyonemus lineatus* larvae. Larvae smaller than 4.64 mm are not included since fin rays and vertebrae are not ossified below this size. Specimens between dashed lines are undergoing notochord flexion.

Standard length (mm)	Vertebrae	Caudal rays		Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Branchiostegal rays (left side)	Gill rakers
		Primary	Secondary						
4.76		4						4	
5.12		4						5	0+0+5
5.56	11	10						7	(not ossified)
6.00	15	13						7	0+0+5
6.12	17	13						7	0+0+5
6.28	18	13						7	0+0+6
6.64	24	17		10	5			7	0+0+9
7.97	25	17	4	XII, 21	I, 11	4		7	3+1+9
10.46	26	17	6	(dam.), 22	II, 11	8	4	7	3+1+12
14.49	26	17	16	XIII, 22	II, 12	17	I, 5	7	4+1+15
32.00	26	17	17	XIV, 21	II, 11	I, 17	I, 5	7	(damaged)

pears at ca. 6.6 mm. By 8 mm additional bones ossified include the epiotic, sphenotic, supraoccipital, parietal, nasal, and the first circumorbital. The skull is essentially complete by ca. 14.5 mm.

None of the bones of the splanchnocranium are ossified at the beginning of the larval stage. By 4 mm they are all ossifying. Teeth first appear at ca. 4.3 mm; four are present on the premaxillary. Four to six dentary teeth are acquired by 5.6 mm; 18 premaxillary teeth are present at this size. Numbers of teeth increase through subsequent larval development: an 8 mm specimen has 26 premaxillary and 18-20 dentary teeth while a 14.5 mm specimen has 60 and more than 30, respectively.

Bones of the suspensorium begin ossifying at ca. 4.2 mm; the hyomandibular and symplectic are first. The ectopterygoid begins to ossify at ca. 6 mm and the quadrate at ca. 6.1 mm. The metapterygoid is next (8 mm). The suspensorium is essentially complete by 14.5 mm.

The opercular apparatus begins ossification at ca. 4 mm with the opercular and preopercular bones. The subopercular is added at ca. 4.2 mm and the interopercle at ca. 4.3 mm. Subsequent development consists of spination and further ossification of these bones.

Ossification of the branchial apparatus commences by 4 mm with the ceratobranchials of the outer two arches. By ca. 4.3 mm the ceratobranchials of four arches are ossified and the hypobranchials are just beginning to ossify. Two pairs of pharyngeal teeth appear at ca. 4.4 mm although the associated pharyngobranchial bones remain unossified until ca. 8 mm. Gill rakers on the outer arch first appear at ca. 5.1 mm—5 lower rakers are present. By 8 mm the number of gill rakers on the outer arch increases to three upper + one at the angle + nine lower rakers. Epibranchials begin to ossify at this size. The basibranchial ossifies between 10.5 and 14.5 mm but the hypohyal remains unossified into the early juvenile stage. The gill raker count at the end of the larval stage is 4+1+15 on the outer arch.

The first three branchiostegal rays are ossifying by 4 mm. A fourth branchiostegal ray and the posterior part of the ceratohyal begin ossification at ca. 4.2 mm; the fifth branchiostegal follows at ca. 4.6 mm. All seven branchiostegals, the epihyal, and interhyal are present by 5.6 mm. Ceratohyal ossification is complete and urohyal ossification is beginning by 6.3 mm. The hyoid apparatus is essentially complete by 14.5 mm, except for the unossified hypohyal.

Vertebral ossification begins with the anterior centra and proceeds posteriorly. Each vertebra ossifies from its ventral midline toward its dorsal midline. Ossification is first evident in a 5.6 mm specimen in the staining of the anterior seven vertebral centra and first four neural arches. In this same specimen centra 8 through 11 are stained ventrally only. By 6 mm the first 10 centra are completely stained, the next 3 on the ventral half only, and the next 2 on the ventral midline only. At this size the first 20 neural arches and 5 haemal arches (originating at the twelfth centrum) are becoming ossified. At 6.3 mm the first 18 centra, 20 neural arches, and 7 haemal arches are stained. By 6.6 mm the anterior part of the urostyle and all except the last centrum are ossified, along with 23 neural arches and 12 haemal arches. The final complement of 25 neural and 14 haemal arches is attained by 8 mm. The first four pleural ribs and three epipleural ribs develop during the transitional period, at ca. 14.5 mm.

The cleithra are the first bones to ossify in the pectoral girdle (by 2.6 mm). The supracleithra begin to ossify at ca. 4.6 mm and the postcleithra at ca. 5.6 mm. The first pectoral radial, coracoid, and scapula begin to stain during the transition to juvenile, after most of the pectoral rays are already ossified. The basipterygia of the pelvic girdle begin to ossify at this time as well.

The general sequence of dorsal and anal fin pterygiophore differentiation is described above under Fin Development. Ossification in both fins begins after 10.5 mm and is completed during the transition to the juvenile stage.

Pterygiophores of the anal spines are fused. Except for the pterygiophores of the first and last soft rays, each successive pair lies between adjacent haemal spines (Fig. 6).

The first two dorsal pterygiophores (bearing the first two dorsal spines) fuse during ossification. The pattern of dorsal pterygiophore placement between adjacent neural spines is somewhat variable (Table 2). Three predorsal bones develop during the transitional period.

The central three hypural elements begin to ossify at ca. 6.1 mm and all hypurals are ossified by 8 mm. These are distinguishable as separate elements throughout larval development. All but one of the principal caudal rays are associated with these elements; the other is associated with the haemal spine of the penultimate vertebra

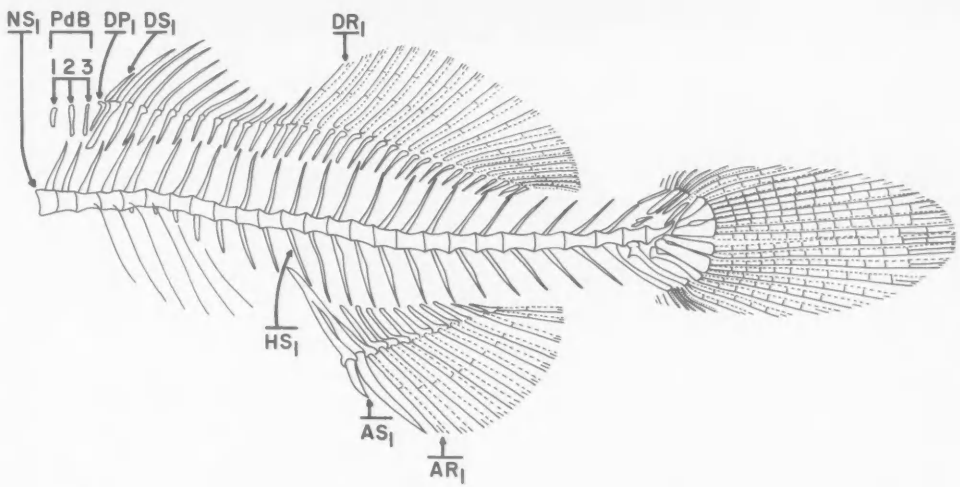

FIGURE 6.—Vertebral column and median fins of a 17.68 mm juvenile *Genyonemus lineatus*, showing typical relationships of dorsal and anal pterygiophores to neural and haemal spines. NS, first neural spine on the first vertebra; PB, predorsal bones; DS, first dorsal spine; DP, first dorsal pterygiophore; DR, first dorsal ray; HS, first haemal spine; AS, first anal spine; AR, first anal ray.

TABLE 2.—Number of dorsal pterygiophores between adjacent neural spines in *Genyonemus lineatus*.

Standard length (mm)	First dorsal pterygiophores	Second dorsal pterygiophores
32	1, 2, 1, 2, 1, 1, 2, 1, 1	1, 2, 2, 2, 2, 3, 2, 3, 2, 3
110	1, 2, 2, 1, 2, 3, 1, 2	2, 2, 2, 2, 2, 2, 2, 3, 2, 1
115	1, 2, 1, 2, 1, 2, 1, 2, 2	1, 2, 3, 2, 2, 2, 3, 2, 3
180	1, 2, 1, 2, 1, 1, 2, 2, 2	2, 2, 2, 3, 2, 2, 3, 3, 1
197	1, 2, 1, 2, 1, 2, 1, 2, 2	2, 2, 3, 2, 1, 3, 2, 3, 1

which is also associated with the first lower secondary caudal ray. Additional lower secondary caudal rays apparently are becoming associated with the haemal spine of the antepenultimate vertebra in specimens larger than 10.5 mm. The first (unossified) epural is associated with the first upper secondary ray at 8 mm. There are five supporting structures above the urostyle in specimens larger than 10.5 mm; the anterior three appear to be associating with the neural spine of the penultimate vertebra, and support five secondary caudal rays. Additional dorsal secondary rays in larger larvae are supported by the neural spine of the antepenultimate vertebra.

Proportions

Larval development of *G. lineatus* is a gradual process without rapid changes in body proportions: all body parts measured are linearly related to standard length through the larval period (Table 3). Since it is of little value to describe such growth only a summary of measurements is given (Table 4).

TABLE 3.—Summary of regressions of measurements of body parts (y) on standard length (x) of *Genyonemus lineatus* larvae.

y	n	r	Regression equation
Head length	164	0.99	$y = -0.24 + 0.32x$
Snout length	155	0.97	$y = -0.10 + 0.09x$
Eye diameter	165	0.98	$y = 0.04 + 0.09x$
Preanal length	166	0.99	$y = -0.51 + 0.59x$
Preanal fin length	85	0.97	$y = 0.20 + 0.62x$
Depth at pectoral insertion	165	0.98	$y = -0.003 + 0.30x$

COMPARISON WITH SIMILAR SPECIES

Genyonemus lineatus eggs closely resemble those of many other fish which spawn in the nearshore coastal waters off southern California. Consequently, separation to the species level is difficult and of doubtful practicality in the routine identification of ichthyoplankton samples.

Among the fish larvae commonly taken in inshore plankton samples along the southern California coast, *G. lineatus* most closely resembles

TABLE 4.—Summary of measurements (in millimeters) of *Genyonemus lineatus* larvae. The mean ($\bar{x}$), sample size (n), and standard deviation (SD) are given for each distance measured. Notochord flexion takes place in the size range demarked by dashed lines.

Size class (SL)	Head length			Snout length			Eye diameter			Preanal length			Preanal fin length			Depth		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD
[1]1.51-2.00	0.48	12	0.06	—			0.20	13	0.02	.98	13	0.05	—			0.68	13	0.02
[1]2.01-2.50	0.46	10	0.03	0.10	10	0.03	0.20	10	0.01	.99	10	0.02	—			0.54	10	0.07
[2]2.51-3.00	0.49	6	0.03	0.13	6	0.02	0.22	6	0.02	1.04	6	0.06	—			0.54	6	0.06
[3]2.01-2.50	0.54	2	0.03	0.14	2	0.03	0.25	2	0.01	1.16	2	0.11	—			0.74	2	0.08
2.51-3.00	0.59	5	0.08	0.13	5	0.04	0.27	5	0.02	1.11	5	0.12	—			0.78	5	0.78
3.01-3.50	0.69	8	0.08	0.20	8	0.05	0.32	8	0.03	1.41	8	0.11	—			0.91	8	0.07
3.51-4.00	0.85	7	0.05	0.21	7	0.04	0.36	7	0.02	1.61	7	0.13	—			1.07	7	0.09
4.01-4.50	1.09	8	0.15	0.28	8	0.06	0.40	8	0.02	1.98	8	0.19	—			1.22	7	0.11
4.51-5.00	1.26	5	0.08	0.36	5	0.02	0.44	4	0.01	2.22	5	0.08	—			1.36	5	0.04
5.01-5.50	1.43	6	0.14	0.37	6	0.10	0.47	6	0.03	2.32	6	0.18	2.93	3	0.37	1.44	6	0.22
5.51-6.00	1.55	9	0.18	0.42	9	0.07	0.53	9	0.06	2.82	9	0.28	3.32	5	0.22	1.81	9	0.20
6.01-6.50	1.78	7	0.20	0.45	8	0.06	0.59	7	0.06	2.98	8	0.23	3.64	5	0.20	1.86	8	0.11
6.51-7.00	1.94	4	0.09	0.43	4	0.04	0.65	4	0.03	3.38	4	0.08	4.05	3	0.08	2.13	4	0.15
7.01-7.50	2.13	5	0.11	0.55	5	0.08	0.70	5	0.05	3.62	5	0.12	4.40	5	0.19	2.21	5	0.06
7.51-8.00	2.31	5	0.19	0.65	5	0.03	0.72	5	0.09	3.97	5	0.29	4.64	4	0.10	2.35	5	0.18
8.01-8.50	2.40	8	0.15	0.66	8	0.09	0.78	8	0.05	4.19	8	0.26	5.05	7	0.35	2.56	8	0.22
8.51-9.00	2.59	5	0.24	0.72	5	0.10	0.81	5	0.06	4.60	5	0.29	5.26	4	0.10	2.78	5	0.17
9.01-9.50	2.73	5	0.14	0.78	5	0.10	0.85	5	0.05	4.72	5	0.24	5.45	5	0.15	2.78	5	0.23
9.51-10.00	2.95	6	0.11	0.78	6	0.10	0.88	6	0.04	5.13	6	0.38	5.86	6	0.21	2.94	6	0.20
10.01-10.50	3.14	9	0.20	0.78	9	0.09	0.93	9	0.05	5.38	9	0.26	5.92	8	0.23	3.08	9	0.11
10.51-11.00	3.22	6	0.06	0.79	6	0.06	0.95	6	0.07	5.83	6	0.23	6.41	6	0.17	3.22	6	0.06
11.01-11.50	3.40	7	0.12	0.93	7	0.07	1.04	7	0.05	6.20	7	0.20	6.73	7	0.18	3.34	7	0.16
11.51-12.00	3.08	1	—	0.83	1	—	0.82	1	—	6.00	1	—	—			3.50	1	—
12.01-12.50	3.68	2	0.22	1.04	2	0.06	1.10	2	0.04	6.53	2	0.16	7.16	1	—	3.51	2	0.01
12.51-13.00	3.83	4	0.26	1.00	4	0.12	1.05	4	0.09	7.15	4	0.21	7.75	4	0.15	3.75	4	0.16
13.01-13.50	4.00	2	0.06	0.96	2	0.11	1.10	2	0.03	7.38	2	0.25	7.96	2	0	3.62	2	0.37
13.51-14.00	4.08	1	—	1.04	1	—	1.20	1	—	7.64	1	—	8.16	1	—	4.12	1	—
14.01-14.50	4.30	2	0.25	1.10	2	0.03	1.22	2	0.08	8.22	2	0.54	8.52	2	0.28	4.20	2	0.45
14.51-15.00	4.72	1	—	1.40	1	—	1.24	1	—	—			—			—		
15.01-15.50	—			—			—			—			—			—		
15.51-16.00	—			—			—			—			—			—		
16.01-16.50	5.24	1	—	1.56	1	—	1.36	1	—	9.32	1	—	10.04	1	—	4.80	1	—
16.51-17.00	—			—			—			—			—			—		
17.01-17.50	6.48	1	—	1.66	2	0.48	1.80	2	0.17	11.74	2	2.46	12.16	2	2.60	5.82	2	0.76
17.51-18.00	—			—			—			—			—			—		
18.01-18.50	4.84	1	—	1.28	1	—	1.32	1	—	8.48	1	—	8.76	1	—	4.32	1	—
18.51-19.00	5.64	1	—	1.60	1	—	1.48	1	—	11.64	1	—	11.96	1	—	5.64	1	—
19.01-19.50	5.20	1	—	1.52	1	—	1.52	1	—	10.40	1	—	10.80	1	—	5.00	1	—
19.51-20.00	5.52	1	—	1.48	1	—	1.68	1	—	11.36	1	—	11.84	1	—	5.80	1	—

[1]Reared specimens, yolk-sac stage.
[2]Reared specimens, postyolk-sac stage.
[3]Field specimens.

the sciaenids *Seriphus politus* and *Roncador stearnsii* (Moser and Butler[5]), the haemulid *Anisotremus davidsonii*, and the scombrid *Scomber japonicus*. *Genyonemus lineatus* is principally a winter spawner while the other species are principally summer spawners, but some overlap occurs in spring and fall.

Scomber japonicus is distinct in having 30-31 myomeres versus 25-26 for the other species. Yolk-sac larvae of *A. davidsonii* are undescribed; however, yolk-sac larvae of the Atlantic haemulids *Haemulon plumierii* (Saksena and Richards 1975) and *Orthopristis chrysoptera* (Hildebrand and Cable 1930) have an anterior oil droplet in contrast with the posterior oil droplet typical of sciaenids. *Seriphus politus* yolk-sac larvae lack the dorsal pigmentation and banded pattern typical of *G. lineatus* (Moser and Butler footnote 5). *Roncador stearnsii* closely resemble *G. lineatus* until late in the yolk-sac stage (Moser and Butler footnote 5) when *G. lineatus* may be distinguished by a single (rarely two) large dendritic nape melanophore extending into the finfold rather than two or more smaller nape melanophores not extending into the finfold. *Roncador stearnsii* typically has heavier anterior gut pigment than *G. lineatus*.

Characters useful for separating *G. lineatus* from similar larvae are summarized in Table 5. The nape melanophore separates *G. lineatus* larvae from *A. davidsonii* and *S. politus* for as long as it remains visible. *Anisotremus davidsonii* may be distinguished from *G. lineatus* to at least as small as 2.6 mm by ventral pigmentation, and by dorsal fin ray counts in older specimens

[5]H. G. Moser, and J. L. Butler. Description of the early life history stages of croakers (Family Sciaenidae) occurring off California. Manuscr. in prep. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038. Pers. commun. February 1981.

TABLE 5.—Selected characters of larvae which resemble *Genyonemus lineatus*.

Species	Myomeres	Dorsal fin rays	Anal fin rays	Preanal lengths (% of SL) mean (range)	Depth (% of SL) mean (range)	Nape melanophore	Melanophore above hindgut	Number of midventral trunk melanophores mode (range)
Anisotremus davidsonii	25-26	XI-XII, 14-16	III, 9-11	[1]48 (43-52)	22 (19-25)	No	Large	14 (12-18)
Genyonemus lineatus	25-26	XII-XV+1, 18-25	II, 10-12	[2]47 (38-53)	30 (26-34)	Yes	Small, often absent	Decreases with growth (2-21)
Roncador stearnsii	25-26	IX-X+1, 21-25	II, 7-9	[3]40 (33-49)	24 (18-31)	Yes	Large	Decreases with growth (5-29)
Seriphus politus	25-26	VII-IX+1, 18-21	II, 21-23	[4]46 (40-54)	26 (23-29)	No	Usually present, usually large	Decreases with growth (2-24)
Scomber japonicus	30-31	VIII-XI+1, 9-14+4-6	II, 9-12+4-6	[5]53 (46-59)	25 (23-27)	No	Two or more	[6]Decreases with growth (10-26)

[1]52 specimens, 2.6-8.1 mm SL.
[2]94 specimens, 2.6-9.7 mm SL.
[3]19 specimens, 2.2-4.3 mm SL.
[4]50 specimens, 3.6-9.8 mm SL.
[5]Taken from Kramer 1960, table 5. Larvae 4.00-9.99 mm SL.
[6]20 specimens, 2.2-5.5 mm SL.

(Table 5). *Anisotremus davidsonii* commonly has a uniform row of one midventral, postanal trunk melanophore per myomere after the first postanal myomere, and nearly always has a large melanophore anteriorly on the ventral midline of the gut. As many as four smaller melanophores may also be arrayed along the midline of the gut. *Genyonemus lineatus*, in contrast, rarely displays uniformity in the midventral, postanal melanophore series (those at myomeres 9-10 and 16-18 typically are distinctly larger), and the ventral gut pigmentation usually is not on the midline. *Genyonemus lineatus* is deeper bodied and its hindgut turns down at a much steeper angle than that of *A. davidsonii*.

Seriphus politus lacks the banded pattern of young *G. lineatus* larvae and usually displays an approximately uniform series of small, postanal midventral melanophores (Moser and Butler footnote 5). Shortly before anal anlage development two melanophores of the midventral series typically enlarge in *S. politus*; these lie at myomeres 11-13 and 19-21 versus 9-10 and 16-18 for *G. lineatus*. During anal fin development the anterior of these migrates internally in *G. lineatus* but remains external in *S. politus*. Specimens smaller than 8 mm are often distinguishable by the presence and size of the melanophore above the hindgut (Table 5). The melanophore on the anterior visceral mass also distinguishes these two after it has assumed its ventral position in *G. lineatus*. *Seriphus politus* larvae are somewhat more slender than *G. lineatus*. Anal fin ray counts separate older specimens.

Roncador stearnsii larvae closely resemble *G. lineatus* (Moser and Butler footnote 5). Before acquisition of fin rays *R. stearnsii* may often be distinguished by having rather heavy anterior gut pigmentation (usually light in *G. lineatus*), by the large melanophore above the hindgut, and by one to three pairs of internal melanophores along either side of the midline of the head behind the eye at the level of the floor of the otic capsule plus one or two medially under the forebrain (these often give the appearance of a stripe through the eye, lacking in *G. lineatus*). Dorsal and anal fin ray counts separate older specimens.

DISTRIBUTION

Genyonemus lineatus off southern California spawns principally from October through April (Skogsberg 1939; Goldberg 1976). This is consistent with our study off San Onofre: larvae were taken from January (initiation of our study) through early June 1978, and early October 1978 through late June 1979, with abundance peaks in March 1978 and February 1979 (Walker et al. footnote 2). Few larvae were taken in June or October.

The smallest larval *G. lineatus* were most abundant in the epibenthos (lower 0.5 m) shoreward of about 3.9 km (21 m isobath) and in the water column above the epibenthos between 2 and 3.9 km from shore (13 and 31 m isobaths). During development, they move shoreward and tend to become more strongly epibenthic. This is evidenced by the low abundance of larvae between ca. 3.8 and 6.4 mm in the water column and offshore of 3.9 km. Larvae larger than 6.4 mm are virtually absent above the epibenthos. The abundance peak for *G. lineatus* larvae larger than ca. 3.8 mm is between 1 and 2 km from shore (9 to 12 m isobaths)[6]. Brewer et al. (in press) noted a similar distribution in their study of the

[6]Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1980. Long term spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS

ichthyoplankton from the shallow coastal waters of the Southern California Bight.

SUMMARY

1) The *G. lineatus* egg is pelagic, transparent, and spherical with an unsculptured chorion, unsegmented yolk and a single clear to yellowish oil droplet. The live egg averages 0.85 mm in diameter and the oil droplet 0.23 mm. Hatching occurs about 52 h after spawning.

2) Yolk-sac larvae hatch at about 1.8 mm in an undifferentiated state with unpigmented eyes, straight tubular gut, large yolk sac, and posterior oil droplet. Pectoral buds develop during the second day after hatching, the mouth opens and gut begins differentiating on the third, eye pigmentation is complete on the fifth, and yolk exhaustion and swim bladder inflation occurs on the sixth.

3) Yolk-sac larvae initially are pigmented primarily on the dorsum. During the yolk-sac period melanophores migrate toward the ventral midline.

4) Pigmentation is largely restricted to the ventrum and dorsal surface of the gut through much of the larval stage. A nape melanophore and the large internal melanophore on the lower anterior midline of the visceral mass are characteristic. A barred pattern develops during the transition to the juvenile stage.

5) The order of ossification (first uptake of alizarin stain) is: cleithra (2.6 mm); splanchnocranium, hyoid apparatus, opercular apparatus, branchial apparatus, skull (4 mm); caudal fin rays (4.8 mm); vertebrae (5.6 mm); second dorsal and anal fin rays and hypural complex (6 mm); first dorsal and pelvic fin rays (7.2 mm); and pectoral fin rays (7.8 mm). Each fin ray begins to ossify before its supporting structure.

6) The principal characters useful for separating *G. lineatus* from similar larvae are the nape melanophore, the anterior visceral mass melanophore when in its ventral position, the larger midventral melanophores at myomeres 9-10 and 16-18, and fin ray and myomere counts.

7) *Genyonemus lineatus* spawns mainly from October through April, with peak spawning in late winter.

8) Larvae are located principally within 4 km from shore. As they develop they tend to move shoreward and into the lower 1 m of the water column.

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ELEMENTAL COMPOSITION (C,N,H) AND ENERGY IN GROWING AND STARVING LARVAE OF *HYAS ARANEUS* (DECAPODA, MAJIDAE)

KLAUS ANGER[1] AND RALPH R. DAWIRS[2]

ABSTRACT

Laboratory-reared larvae of the spider crab, *Hyas araneus* L., were studied with regard to their fresh weight (FW), dry weight (DW), carbon (C), nitrogen (N), hydrogen (H), and energy content (J; estimated from C). FW remains fairly constant in each larval stage, regardless of feeding or starving conditions. This is due to regular changes in water content as opposed to those in organic constitutents. FW therefore is not a good measure for living biomass. Growth in fed zoeal stages, if expressed by gain in any parameter but FW, can be described by power functions of time. There is a considerable gain (by a factor of 2 to 3) within each of these two instars. In the magalopa also a high amount of C, N, H, and energy is accumulated, but most of this gain is lost again during the last third of its stage duration. This finding suggests that there is no more food uptake during this last period preceding metamorphosis to the crab. In all larval stages, weight-specific energy (J/mg DW) follows rather a cyclic pattern with decreases before and after molts, and increases during intermolt periods. It shows a decreasing trend during larval development. The loss in cast exoskeletons is <10% of premolt organic matter in the zoeal stages, but >30% in the megalopa. During starvation, biomass declines in an exponential pattern. Larvae of all stages die, when ca. 40 to 60% of their living substance and energy is lost. The C:N ratio suggests that protein serves as the main source of energy; in the final phase, presumbaly, lipids are also catabolized. Weight-specific energy and probably also metabolism decrease in a hyperbola-shaped curve.

Advanced rearing techniques developed in the last three decades have greatly increased our knowledge of autecology and physiology of meroplanktonic marine larvae. However, there is little quantitative information on growth, energetic needs, and reserves.

Within the literature on decapod larvae, there are numerous data on size increments from one developmental stage to the next (Rice 1968), but few on biomass production. Since size is fairly constant in each particular instar, this information represents only a rough measure of actual growth patterns.

A number of authors have investigated biochemical or energetic aspects of larval development in decapod crustaceans: Reeve (1969), Mootz and Epifanio (1974), Frank et al. (1975), Sulkin et al. (1975), Logan and Epifanio (1978), Morgan et al. (1978), Anger and Nair (1979), Capuzzo and Lancaster (1979), Omori (1979), Dawirs (1980), Stephenson and Knight (1980). These studies, however, mainly concentrated on gross differences among larval stages rather than on changes within single instars. Thus, biomass was either considered practically constant in each stage, or it was interpolated by means of (mostly exponential) regression equations describing growth from the first to the last larval instar. The present paper attempts to analyze actual growth patterns within stages of the spider crab, *Hyas araneus*.

Growth achieved in the laboratory under optimal food conditions (as in this paper) probably represents only one end of the scope in which development is possible, rather than a typical expression of it. The other end is characterized by the poorest food level still allowing minimal growth. Anger and Dawirs (1981) discussed the potential ecological role of starvation in a variable environment. They showed that larvae of *Hyas araneus* are well adapted to this condition.

In the present study diminution and growth rates were estimated from frequent samples of starved and fed larvae. They constitute a further step toward a better understanding of larval ecology and energetics in North Sea species as required in a joint research project (Anger and

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Nair 1979; Dawirs 1979, 1980; Anger and Dawirs 1981).

MATERIALS AND METHODS

Ovigerous *Hyas araneus* were dredged from a deep channel near the island of Helgoland (North Sea) during early winter in 1978-79 and 1979-80. After hatching, the zoeae were isolated in vials and maintained individually at 12°C. Food (a mixture of freshly hatched Australian *Artemia* sp. nauplii and the rotifer *Brachionus plicatilis*) and filtered seawater were changed every second day. The methods of obtaining and rearing the larvae have been described in detail by Anger and Dawirs (1981).

For determination of wet weight, larvae were caught individually with pen-steel forceps, briefly rinsed in water from an ion exchanger, blotted for about 10 s on filter paper, and transferred to preweighed silver cartridges. All weight measurements were carried out on an Autobalance AD-2 (Perkin-Elmer)[3] to the nearest 0.1 μg. The techniques and equipment used for obtaining dry weight (DW), carbon (C), nitrogen (N), and hydrogen (H) content of larvae and young crabs were the same as described by Anger and Nair (1979) and Dawirs (1980): deep freezing, vacuum drying, weighing, and combustion in a C-H-N analyzer (Model 1106, Carlo Erba Science). Only rinsing of the material (see above) was added as an initial step. This standard procedure was adopted to remove possible adherent salt and thus to increase the accuracy of the measurements. Comparison of test measurements, however, did not show significant differences (Anger and Nair 1979).

Energy estimates (J) were obtained from carbon values by applying the N-corrected regression equation given by Salonen et al. (1976). Statistical procedures were the same as referred to in detail by Anger and Dawirs (1981). In regression equations, intercept (b) and slope (m) are given; in addition, correlation coefficients (r) and their level of significance (P) for deviation from zero are provided. For logarithmic transformations, ln (= $\log_e$) was applied. All statistical tests were two-tailed.

In May 1979, a first series of 46 analyses comprising 123 individually reared zoea-1 larvae (Z-1) of *Hyas araneus* was carried out to compare their growth patterns with those previously observed by Anger and Nair (1979) in commonly reared zoeae. This set of data showed unsatisfactorily high variation, and high mortality prevented a larger number of analyses. For this reason, in February 1980 another set of 92 analyses comprising 110 prezoeae, 274 Z-1, and 30 early Z-2 was obtained (Table 1). The data for later stages given in Table 2 had been obtained in March and April 1979 (112 samples, 149 individuals).

RESULTS

Larval Growth

Fresh weight (FW) values fluctuated around constant levels in all larval stages without clear increase in a single stage (Tables 1, 2). This steplike growth pattern did not allow any analysis of actual body growth during larval instars.

The gain in total live weight (FW) from the prezoea to the freshly metamorphosed crab was ca. 770%. It was 640% in DW, and only ca. 470% in C, N, and H. The absolute increase during larval development is shown in Figure 1. During the extremely short, nonfeeding prezoea stage there was no gain in C, N, H, and energy. Molting to the Z-1 resulted in a minor loss of organic constituents (cast cuticle) and in some uptake of water and salt (Table 1; Fig. 1). During the following instars there was an appreciably absolute increase in all parameters considered. It was generally strongest in the second zoeal stage and, surprisingly, weakest in the megalopa.

The values shown in Figure 1 for Z-1, Z-2, and magalopa form a straight line when arranged in a semilogarithmic scale. This indicates that growth from stage to stage followed an exponential pattern during this period.

The different growth patterns in wet weight (steplike) and DW (gradual) were caused by a combination of these two patterns in the water content of the larvae; during each molt, it suddenly increased, and then it gradually decreased during the molt cycle. This decrease could be expressed as a power function in all larval instars: $\ln (\% H_2O) = b + m \ln (t+1)$, where b is approximately the logarithm of the initial water content, m is the slope, and t is the time (days from the beginning of a particular stage). All r's for these fitted curves were significantly different from zero ($P<0.001$). The rate of de-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—*Hyas araneus* larval growth. Fresh weight (FW), dry weight (DW), water content (H_2O), carbon (C), nitrogen (N), hydrogen (H), C:N ratio (C/N, by weight), energy content (Joule, J), number of analyses (*n*), and number of individuals analyzed (*N*). Mean values ±95% confidence intervals.

			Prezoea	Zoea 1														Zoea 2	
	Time (d):		0	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1
FW		$\bar{x}$	338	493	537	536	558	563	575	560	583	604	607	618	594	595	606	1,008	1,076
	(μg)	±	9	10	22	28	10	22	26	27	12	10	21	42	26	17	—	48	131
DW		$\bar{x}$	57	65	95	108	122	134	142	141	155	153	166	166	174	167	170	168	189
	(μg)	±	3	1	4	5	5	4	5	7	2	3	6	6	6	6	—	6	10
H_2O	(%)		85.6	86.8	82.4	79.8	78.1	76.1	75.2	74.8	73.5	74.7	72.8	73.2	70.7	71.9	71.9	83.3	82.4
C	(%)	$\bar{x}$	41.9	35.1	32.2	32.0	33.2	34.0	35.8	36.7	36.7	39.3	39.0	40.4	40.5	40.4	40.0	38.7	36.1
		±	0.5	0.3	0.5	0.2	0.5	0.3	0.6	0.5	0.6	0.5	0.4	0.5	0.6	0.8	—	0.8	1.0
	(μg)	$\bar{x}$	23.9	22.9	30.5	34.6	40.6	45.9	50.9	51.8	56.8	60.1	64.6	67.1	70.5	67.5	68.1	65.1	68.1
		±	1.3	0.3	1.9	1.6	1.4	1.2	2.8	2.8	1.2	1.3	3.0	2.3	3.4	3.6	—	1.2	3.6
N	(%)	$\bar{x}$	10.6	8.1	6.7	6.4	6.5	6.4	6.7	7.0	7.2	7.6	7.6	8.1	8.3	8.3	8.3	8.3	7.6
		±	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.3	0.2	0.2	0.1	0.1	0.2	—	0.1	0.2
	(μg)	$\bar{x}$	6.0	5.3	6.4	6.9	8.0	8.7	9.5	9.9	11.0	11.6	12.7	13.4	14.0	14.0	14.2	13.9	14.3
		±	0.3	0.1	0.4	0.3	0.2	0.3	0.4	0.4	0.5	0.1	0.6	0.6	0.5	0.7	—	0.2	0.6
H	(%)	$\bar{x}$	6.6	5.0	4.8	4.7	4.9	5.1	5.2	5.6	5.6	5.9	5.8	6.1	6.3	6.2	6.0	6.1	5.6
		±	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.2	—	0.1	0.2
	(μg)	$\bar{x}$	3.8	3.3	4.5	5.1	6.0	6.9	7.4	7.9	8.6	9.0	9.7	10.1	10.9	10.4	10.6	10.3	10.6
		±	0.2	0.1	0.4	0.2	0.2	0.1	0.4	0.5	0.3	0.3	0.5	0.3	0.6	0.7	—	0.2	0.6
C/N		$\bar{x}$	3.9	4.3	4.8	5.0	5.1	5.3	5.3	5.2	5.2	5.2	5.1	5.0	5.0	4.9	4.8	4.7	4.8
		±	0.1	0.03	0.04	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.05	—	0.1	0.1
J/ind.		$\bar{x}$	0.89	0.79	1.01	1.15	1.37	1.56	1.77	1.82	1.99	2.17	2.33	2.46	2.59	2.48	2.49	2.34	2.37
		±	0.05	0.01	0.06	0.05	0.05	0.04	0.11	0.10	0.05	0.05	0.12	0.08	0.11	0.15	—	0.03	0.14
J/mg DW		$\bar{x}$	15.6	12.1	10.7	10.6	11.2	11.5	12.4	12.8	12.9	14.1	14.0	14.8	14.9	14.8	14.6	13.9	12.6
		±	0.9	0.2	0.2	0.1	0.3	0.2	0.3	0.2	0.3	0.3	0.2	0.03	0.4	0.4	—	0.4	0.5
n (analyses)			11	10	5	5	5	5	5	5	5	5	5	5	5	5	1	5	5
N (individuals)			110	50	25	25	25	25	15	15	15	15	15	15	15	15	4	15	15

TABLE 2.—*Hyas araneus* larval growth. For explanation of abbreviations see Table 1.

		Zoea 2					Megalopa							Crab 1		
Time (d):		0	1	4	8	11	0	4	8	12	16	20	24	0	1	2
FW	$\bar{x}$	994	1,150	1,206	1,011	1,094	2,289	1,861	1,961	2,163	2,496	2,187	1,872	2,926	3,597	4,065
(μg)	±	36	308	236	108	31	236	97	180	461	395	297	153	330	238	577
DW	$\bar{x}$	144	172	253	280	291	333	428	517	576	656	576	450	424	622	902
(μg)	±	7	27	25	25	11	55	88	92	170	57	125	62	87	51	135
H_2O (%)		87.3	86.9	82.7	78.3	79.0	87.3	81.3	79.2	79.0	79.2	79.2	80.6	87.3	85.2	77.8
C (%)	$\bar{x}$	32.2	37.5	35.5	36.8	38.5	35.6	30.4	32.6	31.4	33.2	33.6	31.1	33.5	32.4	29.3
	±	1.2	2.7	1.8	1.2	0.6	2.0	0.9	1.8	3.1	2.2	2.2	2.0	1.7	0.7	3.5
(μg)	$\bar{x}$	46.3	62.8	89.7	103.3	111.9	118.9	130.5	169.8	183.6	218.3	195.0	141.2	137.3	201.1	264.5
	±	2.1	11.2	12.3	12.1	5.5	21.9	29.9	36.5	70.8	28.9	56.1	28.5	26.4	16.1	47.7
N (%)	$\bar{x}$	8.0	8.4	7.6	8.2	8.5	8.2	6.2	7.0	7.1	7.9	7.8	7.0	8.3	7.8	6.4
	±	0.3	0.2	0.3	0.2	0.2	0.5	0.1	0.4	0.5	0.2	0.5	0.3	0.6	0.3	1.1
(μg)	$\bar{x}$	11.6	14.4	19.2	23.0	24.6	27.1	26.5	36.5	41.6	51.9	45.1	31.6	34.9	48.2	57.7
	±	0.2	2.0	2.1	2.3	1.2	4.2	5.6	7.9	14.3	5.5	13.0	5.7	5.5	3.4	11.3
H (%)	$\bar{x}$	4.8	5.7	5.2	5.5	5.7	5.3	4.6	5.0	4.8	5.2	5.2	4.9	4.9	4.9	4.3
	±	0.2	0.2	0.3	0.2	0.1	0.4	0.1	0.4	0.5	0.2	0.4	0.4	0.3	0.2	0.6
(μg)	$\bar{x}$	6.9	9.8	13.2	15.5	16.7	17.8	19.9	26.0	28.0	34.0	30.4	22.1	20.8	30.2	39.1
	±	0.4	1.5	1.9	2.1	1.0	3.4	4.6	6.3	10.6	4.2	8.9	4.5	4.0	2.3	7.3
C/N	$\bar{x}$	4.0	4.4	4.6	4.5	4.5	4.4	4.9	4.6	4.4	4.2	4.3	4.4	3.9	4.2	4.6
	±	0.1	0.2	0.1	0.2	0.1	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.2	0.1	0.3
J/ind.	$\bar{x}$	1.54	2.20	3.11	3.64	4.02	4.14	4.25	5.70	6.09	7.37	6.63	4.66	4.58	6.71	8.49
	±	0.08	0.42	0.47	0.48	0.22	0.81	1.02	1.31	2.58	1.15	2.10	1.06	0.88	0.54	1.77
J/mg DW	$\bar{x}$	10.7	12.8	12.1	13.0	13.8	12.4	9.9	10.9	10.4	11.2	11.4	10.3	10.9	10.8	9.4
	±	0.6	1.5	0.8	0.6	0.3	1.0	0.4	0.8	1.5	1.1	1.1	0.9	0.7	0.4	1.6
n (analyses)		10	3	11	8	14	9	5	7	5	5	5	7	6	13	4
N (individuals)		41	9	11	8	14	9	5	7	5	5	5	7	6	13	4

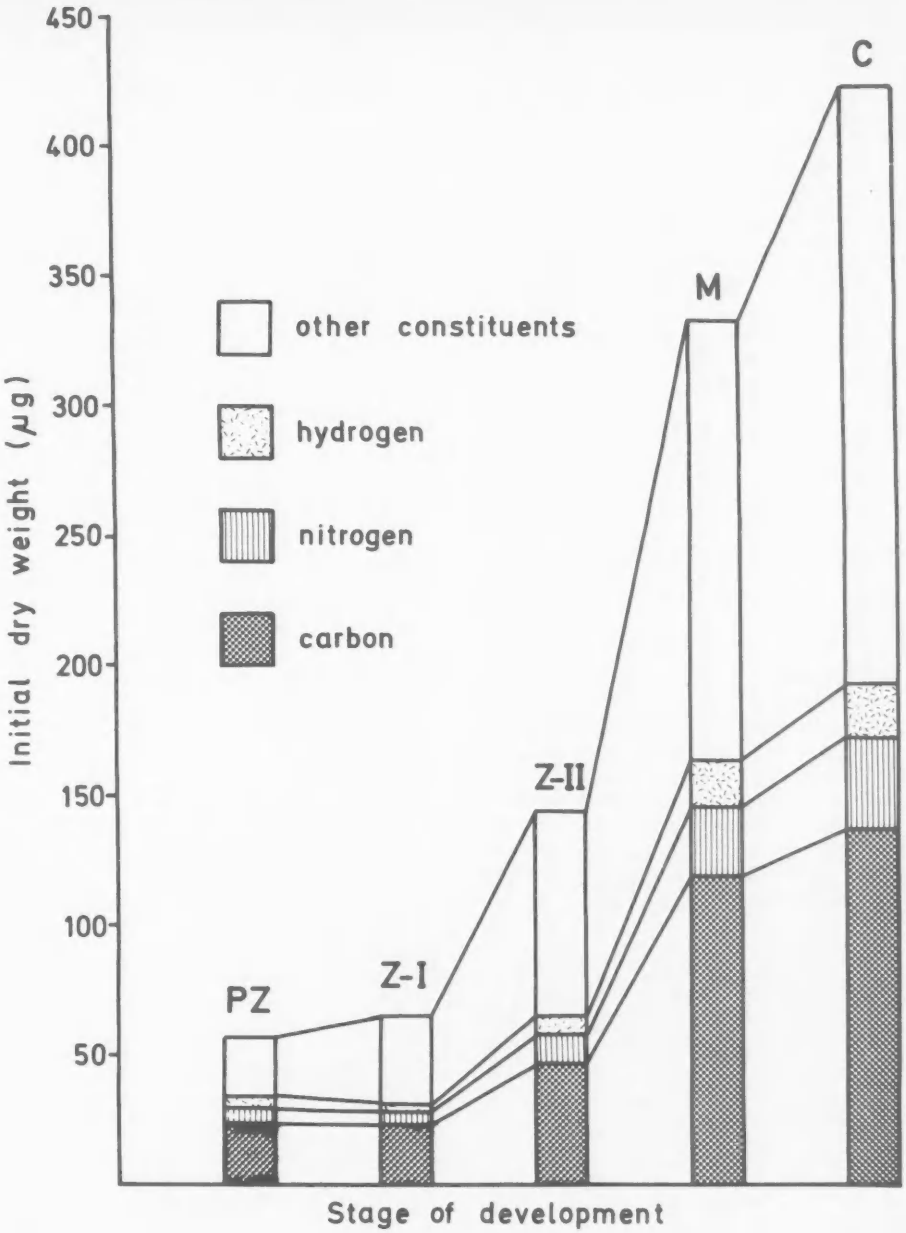

FIGURE 1.—*Hyas araneus*. Initial dry weight, carbon, nitrogen, and hydrogen content in the prezoea (PZ), zoeal stages (Z-I, Z-II), megalopa (M), and first crab stage (C).

crease gradually declined during larval development (Tables 1, 2). This trend was reflected by decreasing m of fitted regression curves: −0.074 in the Z-1, −0.045 in the Z-2, and −0.031 in the megalopa. In Figure 2 only the first regression (Z-1) is shown as the most accurately measured example (the curve for starved zoeae given in the same graph will be discussed below).

Growth in zoeal stages can also be described as a power function of t: $\ln y = b + m \ln(t+1)$, where y is any measure of biomass except FW (DW, C, N, H, J). The b values were almost identical with the logarithms of the initial biomass measure under consideration, the m values varied between 0.29 and 0.48 (Table 3).

The fitted curves describe the actual growth patterns until late premolt was reached. In this very advanced period in the Z-1 stage (days 12 and 13), growth ceased or even switched to a slight loss. These last values were not included in the Z-1 regressions. The fitted growth curves were converted to percentage values of early postmolt levels, so that direct comparison of relative increase rates became possible (Fig. 3; Z-1 curves for 1980 values only).

In zoeae the individual energy content (J) revealed the strongest increment, DW the weakest. The rate of increase in N was similar to that in DW, whereas C and H increased at a higher rate during individual growth (Table 3). A comparison of the biomass values in first zoeae obtained in two different seasons and years shows that the 1979 larvae were not only less viable (see above), but also showed lower initial biomass (reflected by lower b values in all regression equations describing growth) and lower growth rates (reflected by m values), especially in C, H, and J.

TABLE 3.—Parameters of regression equations for individual growth in larval stages of *Hyas araneus*: $\ln y = b + m \cdot \ln(t+1)$. t = time (d); r = correlation coefficient; df = degrees of freedom; dry weight (DW), carbon (C), nitrogen (N), hydrogen (H) in μg, and energy contents (J).

Stage	y	b	m	r	df
Zoea I[1]	DW	4.164	0.300	0.924	44
Zoea I	DW	4.228	0.385	0.989	64
Zoea I[1]	C	2.918	0.370	0.873	44
Zoea I	C	3.107	0.451	0.994	64
Zoea I[1]	N	1.495	0.331	0.839	44
Zoea I	N	1.604	0.384	0.979	60
Zoea I[1]	H	1.016	0.354	0.833	44
Zoea I	H	1.164	0.475	0.994	62
Zoea I[1]	J	−0.511	0.377	0.870	44
Zoea I	J	−0.292	0.479	0.990	64
Zoea II	DW	4.986	0.290	0.938	44
Zoea II	C	3.858	0.354	0.934	44
Zoea II	N	2.449	0.305	0.938	44
Zoea II	H	1.961	0.350	0.925	44
Zoea II	J	0.457	0.381	0.927	44

[1]1979 observation (all others from 1980).

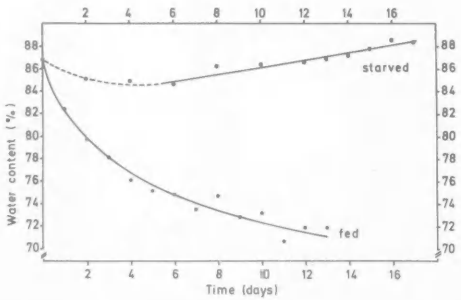

FIGURE 2.—*Hyas araneus*. Water content (% fresh weight) in Z-1 larvae fed and starved for different lengths of time.

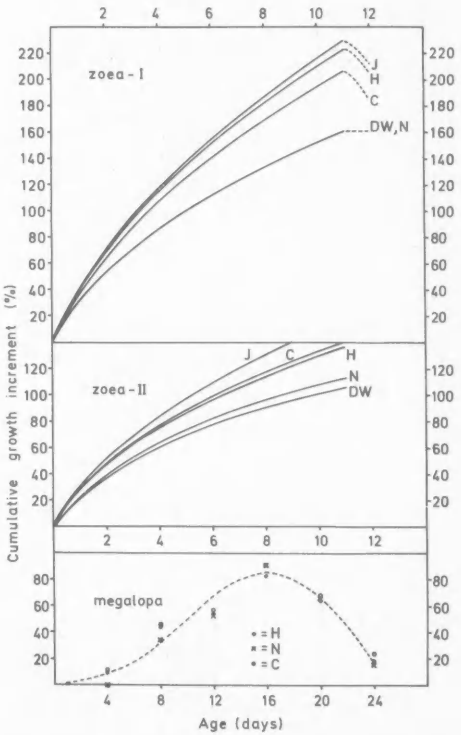

FIGURE 3.—*Hyas araneus*. Growth patterns [dry weight (DW), energy contents (J), carbon (C), nitrogen (N), and hydrogen (H) per individual] in all larval stages expressed as percentage of early postmolt levels. Solid curves: fitted by equations (see text); dotted curves: fitted by eye.

However, due to high variation among the 1979 samples, these differences were not statistically significant.

In May 1979, eight Z-2 of *H. araneus* were isolated from a plankton sample and analyzed for comparison. The results (Table 4) compared favorably with those of late laboratory-reared Z-2 larvae (Table 2), although C and H values were slightly higher in the field-caught larvae.

It becomes obvious from Figure 3 (lower graph) that growth in the megalopa was quite different from that in the zoeal stages. Since variation among analyses (see Table 2) was rather high, calculation of fitted growth curves was not considered useful and, therefore, only the assumed pattern was displayed in the diagram as an eye-fitted curve. A surprising decrease in all parameters was found during the last third of the megalopa stage. As a result, young crabs contained only little more organic substances than young megalopae (Fig. 1).

From the above results, approximate average daily energy gains per individual (J/d per ind.) can be calculated. In the 1979 Z-1 larvae a value of 0.08 was estimated. This compares favorably with the data reported by Anger and Nair (1979). They found 0.06 (their figures −0.4 and 0.6 on page 51 are erroneous; they should read −0.04 and 0.06), based on C contents, and 0.07 to 0.11, based on biochemical composition (excluding and including chitin, respectively). Since the 1980 larvae grew better (see above), their daily energy gain was higher: 0.16 J/d per ind. In the second zoeal stage a value of 0.22 was found (Fig. 1). In the megalopa it was similar (0.20) until day 16, when it dropped to −0.34 until metamorphosis; on the average, a weak gain (0.02 J/d per ind.) resulted.

TABLE 4.—Ranges and arithmetic means ($\bar{x}$) for *Hyas araneus* zoea-2 from Helgoland plankton in May 1979. Four analyses comprising eight individuals. For explanation of abbreviations see Table 1.

		Range	$\bar{x}$
FW	(µg)	1,162-1,292	1,220
DW	(µg)	304-346	322
H_2O	(%)	72.6-74.4	73.6
C	(%)	35.0-36.9	35.7
	(µg)	106.7-127.4	115.2
N	(%)	7.60-7.73	7.67
	(µg)	23.1-26.7	24.7
H	(%)	5.23-5.51	5.36
	(µg)	15.9-19.0	17.3
C/N		4.53-4.77	4.66
J/ind.		3.67-4.49	4.00
J/mg DW		12.1-13.0	12.4

The weight-specific energy content (J/mg DW) followed a cyclic pattern (Fig. 4). Due to salt uptake, it decreased during molt, and then it increased again during growth. From instar to instar there was a conspicuous decreasing trend. It was related to a decrease in the percentage of organic substances, expressed as maximum sum of the C, N, and H portions (upper part of Fig. 4).

The ratio between single elements can be used as an index for biochemical composition. Changes in the C:N ratio mainly indicate shifts in the relative amounts of lipids (plus carbohydrates) and proteins (plus free amino acids) (Fig. 5). There were no major differences found during the molt cycles. In all larval stages there was an initial increase, followed by a decline.

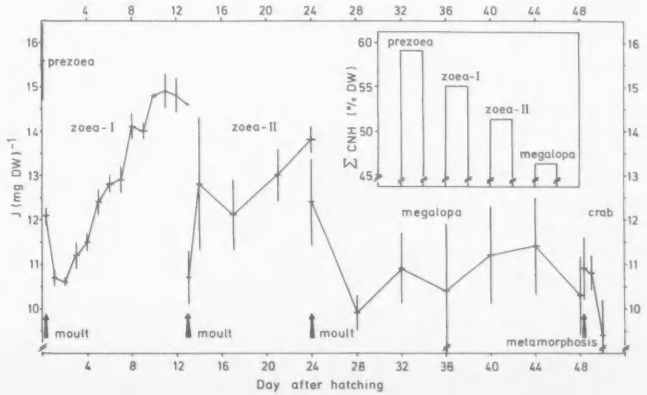

FIGURE 4.—*Hyas araneus*. Changes in weight-specific energy during larval development; vertical lines: 95% confidence intervals of the means. Upper right: Maximum sum of carbon (C), nitrogen (N), and hydrogen (H) in all larval stages.

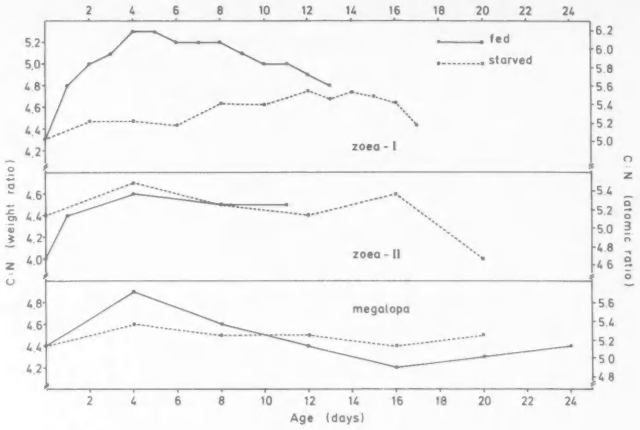

FIGURE 5.—*Hyas araneus*. C:N (carbon:nitrogen) ratio in larvae fed and starved for different lengths of time.

Certainly the buildup of the chitin cuticle, and perhaps also the disproportionately strong storage of lipids, contributed to the increase. The subsequent decrease in the C:N ratio suggests that more proteins than other organic constituents were accumlated later. This trend was best visible in the Z-1 and megalopa stages; in the latter it was followed by a new increase beginning on day 16. This period was identical with that of decreasing biomass (Fig. 3). The curves given in Figure 5 for starved larvae will be discussed below.

The C:H ratio remained fairly constant within stages, and it did not differ much among larval instars. The mean values and 95% confidence intervals (weight-based) were 6.67±0.08 in the Z-1 (1980), 6.64±0.26 in the Z-2, and 6.49±0.11 in the megalopa. In field-caught Z-2 larvae and in young crabs mean ratios of 6.66 and 6.67 were found. The ratios in the Z-1 and megalopa stages were statistically different from each other ($P<0.01$). There was also a significant difference ($P = 0.002$) between the figures in the Z-1 from 1979 (6.86±0.09) and from 1980 (see above).

The growth patterns described in Figure 3 do not consider losses due to shedding of exuviae. In order to determine the approximate amount of organic substances cast during molts, occasional analyses of exuviae were carried out (Table 5). Wet weight and DW measurements did not provide useful results, because the amount of water and salt inside the cast could not be accurately determined. The composition of the exuviae corresponded closely to that of its main component, chitin. Deviations from the theoretical atomic ratio C:N:H = 9:1:14 can partly be explained by analytical inaccuracies (see 95% confidence limits in the megalopa), partly by other biochemical components of exuviae, or by slight chemical changes before sampling and analyzing the casts (partial decomposition).

The amount of organic matter lost during zoeal molts was far lower than during metamorphosis to the crab: 4 to 5% versus 19% in N, 6 to 9% versus 29% in both C and H (Table 5). Assuming an energy content of ca. 18 J/mg dry organic exuvial matter (after Winberg 1971, somewhat corrected for protein compounds) and a C content of ca. 45% (according to the molecular formula of chitin), then the energy losses should be ca. 0.23 J in the Z-1, 0.29 in the Z-2, and 1.61 in the megalopa. These estimates correspond to ca. 9, 7, and 34% of total body energy levels in late premolt in these stages. Compared with average daily energy fixation rates (see above), these figures mean losses of ca. 1.3 to 1.4 d in the zoeal stages, and ca. 8 d in the megalopa.

Preliminary experiments were carried out to

TABLE 5.—Composition [carbon (C), nitrogen (N), hydrogen (H)] of larval exuviae of *Hyas araneus* and percentage of premolt matter cast at ecdysis. n = number of analyses, N = number of exuviae analyzed.

	C (µg)	N (µg)	H (µg)	Weight ratio	Atomic ratio	n	N
Zoea-I	5.85	0.67	0.92	8.7:1:1.4	10:1:19	1	15
% cast	9	5	9				
Zoea-II	7.20	1.10	1.10	6.6:1:1	8:1:14	1	10
% cast	6	4	7				
Megalopa $\bar{x}$	40.56	5.46	6.39	7.5:1:1.2	9:1:16	7	7
±	4.07	0.62	0.56				
% cast	28	17	29				

determine food consumption in the Z-1 stage using *Artemia salina* nauplii as prey. The average values found were near 20 μg C/d per ind. or 0.8 to 0.9 J/d. Gross growth efficiency therefore should be about 10 to 20%. The amount taken up by the larvae (3 d old) corresponded to ca. 55% of their own body C and to ca. 36% of their own DW. In light of the experimental conditions, we consider this near the maximum level.

Loss of Biomass During Starvation

FW of starving larvae did not show significant changes (Tables 6 to 8). Also water content could not always be measured with sufficient accuracy to detect clear trends. In the Z-1 and in the megalopa, first a slight decrease and later a conspicuous increase of water content occurred. The latter trend was linear in the Z-1 (Fig. 2); it could

TABLE 6.—*Hyas araneus* losses in starved Z-1 larvae. For explanation of abbreviations see Table 1.

Time (d):		0	2	4	6	8	10	12	13	14	15	16	17
FW	$\bar{x}$	493	538	522	501	534	533	532	557	547	577	584	589
(μg)	±	10	16	27	20	16	29	38	14	28	52	35	39
DW	$\bar{x}$	65	80	79	77	74	73	71	73	70	70	66	68
(μg)	±	1	2	3	3	3	2	2	3	1	2	1	4
H_2O (%)		86.8	85.1	84.9	84.6	86.2	86.4	86.6	86.9	87.2	87.8	88.6	88.4
C (%)	$\bar{x}$	35.1	27.5	25.8	24.7	24.6	23.2	22.8	22.0	22.2	21.7	22.1	21.4
	±	0.3	0.4	0.3	0.2	0.3	0.4	0.6	0.3	0.3	0.4	0.3	1.0
(μg)	$\bar{x}$	22.9	21.9	20.4	19.0	18.2	16.8	16.2	16.1	15.6	15.3	14.6	14.6
	±	0.3	0.2	0.7	0.7	0.8	0.5	0.8	0.8	0.2	0.5	0.4	0.7
N (%)	$\bar{x}$	8.1	6.2	5.8	5.57	5.3	5.0	4.8	4.72	4.7	4.6	4.8	4.8
	±	0.1	0.1	0.1	0.04	0.2	0.2	0.2	0.05	0.1	0.1	0.1	0.2
(μg)	$\bar{x}$	5.3	4.91	4.6	4.3	3.9	3.6	3.4	3.4	3.30	3.26	3.16	3.3
	±	0.1	0.04	0.1	0.2	0.2	0.1	0.2	0.1	0.06	0.07	0.03	0.1
H (%)	$\bar{x}$	5.0	3.82	3.55	3.60	3.33	3.27	3.15	3.11	3.17	3.3	3.2	3.0
	±	0.1	0.05	0.05	0.04	0.04	0.07	0.11	0.06	0.02	0.3	0.1	0.4
(μg)	$\bar{x}$	3.3	3.05	2.8	2.8	2.5	2.4	2.2	2.3	2.23	2.2	2.1	2.1
	±	0.1	0.02	0.1	0.1	0.1	0.1	0.1	0.1	0.02	0.1	0.1	0.1
C/N	$\bar{x}$	4.31	4.47	4.47	4.43	4.63	4.62	4.75	4.67	4.74	4.70	4.64	4.43
	±	0.03	0.04	0.04	0.06	0.12	0.10	0.11	0.09	0.07	0.05	0.11	0.05
J/ind.	$\bar{x}$	0.79	0.69	0.62	0.57	0.55	0.50	0.48	0.47	0.45	0.44	0.42	0.42
	±	0.01	0.01	0.02	0.02	0.02	0.01	0.02	0.02	0.01	0.02	0.01	0.02
J/mg DW	$\bar{x}$	12.1	8.6	7.9	7.4	7.4	6.8	6.7	6.4	6.5	6.3	6.4	6.1
	±	0.2	0.3	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.4
n (analyses)		10	5	5	5	5	5	5	5	5	5	5	3
N (individuals)		50	25	25	25	25	25	25	25	25	25	25	13

TABLE 7.—*Hyas araneus* losses in starved Z-2 larvae. For explanation of abbrevations see Table 1.

Time (d):		0	4	[1]4	8	[1]8	12	[1]12	16	20
FW	$\bar{x}$	1,150	2,422	1,219	1,184	1,176	1,034	1,022	929	1,240
(μg)	±	308	349	68	102	67	144	—	263	474
DW	$\bar{x}$	172	174	195	145	170	154	172	153	131
(μg)	±	28	14	15	17	24	12	—	17	14
H_2O (%)		85.0	92.8	84.0	87.8	85.5	85.1	83.2	83.5	89.4
C (%)	$\bar{x}$	36.5	29.9	30.4	28.2	27.2	26.7	26.6	25.5	22.2
	±	2.7	1.2	1.9	1.4	1.7	2.2	—	1.4	2.1
(μg)	$\bar{x}$	62.8	52.1	59.6	40.8	46.5	41.1	45.6	39.0	29.0
	±	11.2	6.0	8.1	5.6	9.0	5.6	—	5.9	5.4
N (%)	$\bar{x}$	8.4	6.4	7.0	6.3	6.4	6.1	6.3	5.6	5.5
	±	0.3	0.3	0.7	0.8	0.3	0.1	—	0.3	0.4
(μg)	$\bar{x}$	14.4	11.1	13.5	9.1	10.9	9.7	10.9	8.6	7.2
	±	1.9	1.3	2.2	1.9	1.9	0.9	—	0.9	1.3
H (%)	$\bar{x}$	5.7	4.3	4.2	3.9	3.7	3.8	3.8	3.7	3.1
	±	0.3	0.2	0.4	0.4	0.3	0.4	—	0.2	0.4
(μg)	$\bar{x}$	9.8	7.5	8.2	5.6	6.3	6.2	6.5	5.6	4.1
	±	1.6	0.8	1.3	1.0	1.3	0.8	—	0.8	0.9
C/N	$\bar{x}$	4.4	4.7	4.4	4.5	4.3	4.4	4.2	4.6	4.0
	±	0.3	0.1	0.3	0.5	0.3	0.4	—	0.3	0.1
J/ind.	$\bar{x}$	2.2	1.7	1.9	1.3	1.4	1.3	1.4	1.2	0.8
	±	0.4	0.2	0.3	0.2	0.3	0.2	—	0.2	0.2
J/mg DW	$\bar{x}$	12.8	9.6	9.9	8.9	8.5	8.2	8.2	7.8	6.4
	±	1.0	0.6	0.9	0.6	0.7	1.0	—	0.6	0.8
n (analyses)		3	5	5	5	5	5	2	5	5

[1]Analyses of group maintained larvae.

TABLE 8.—*Hyas araneus* losses in starved megalopa larvae. For explanation of abbreviations see Table 1.

	Time (d):	0	4	8	12	16	20
FW	$\bar{x}$	2,289	2,131	1,963	2,200	2,275	2,370
(μg)	±	236	192	268	280	158	406
DW	$\bar{x}$	333	327	309	358	304	281
(μg)	±	55	55	74	103	96	106
H_2O	(%)	85.4	84.7	84.3	83.7	86.6	88.2
C	(%) $\bar{x}$	35.6	25.8	23.3	23.1	23.0	22.8
	±	2.0	0.6	1.0	1.2	1.6	1.1
(μg)	$\bar{x}$	118.9	84.7	72.2	83.1	70.5	64.0
	±	21.9	16.3	17.9	27.7	26.8	26.7
N	(%) $\bar{x}$	8.2	5.6	5.1	5.1	5.2	5.1
	±	0.5	0.3	0.3	0.1	0.3	0.3
(μg)	$\bar{x}$	27.1	18.4	15.9	18.4	15.9	14.2
	±	4.2	3.6	3.8	5.6	5.2	4.6
H	(%) $\bar{x}$	5.3	3.7	3.4	3.5	3.3	3.5
	±	0.4	0.2	0.2	0.3	0.2	0.3
(μg)	$\bar{x}$	17.8	12.0	10.5	12.6	10.2	9.8
	±	3.4	2.5	2.7	4.5	3.7	4.7
C/N	$\bar{x}$	4.4	4.6	4.5	4.5	4.4	4.5
	±	0.2	0.2	0.1	0.2	0.3	0.5
J/ind.	$\bar{x}$	4.1	2.6	2.1	2.4	2.1	1.9
	±	0.8	0.5	0.5	0.9	0.8	0.8
J/mg DW	$\bar{x}$	12.4	7.9	6.9	6.8	6.8	6.7
	±	1.0	0.3	0.4	0.5	0.6	0.4
n (analyses)		9	5	5	5	5	3

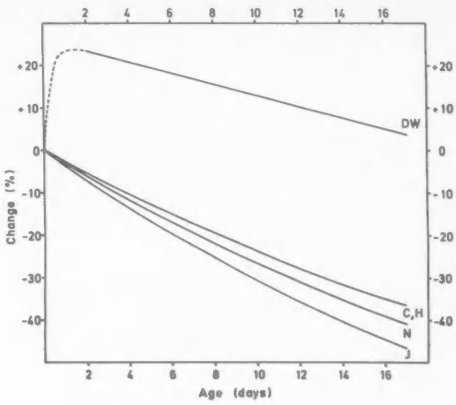

FIGURE 6.—*Hyas araneus*. Loss patterns [dry weight (DW), energy content (J), carbon (C), nitrogen (N), and hydrogen (H) per individual] in starved Z-1 larvae. Solid lines: fitted by equations (see text); dotted curve: fitted by eye.

be expressed by the statistically significant regression equation: $\%H_2O = 83 + 0.32\ t$ ($r = 0.959$; $P<10^{-4}$), where t = time (days from hatching). This effect was visible by eye: larvae, which had starved for a long time, acquired an increasingly bloated appearance like those exposed to a hypotonic medium.

DW tended to decrease during starvation, but due mostly to high variation among parallel determinations, only in the Z-1 stage could a statistically significant trend be found between days 2 and 17 (Fig. 6): $DW\ (\mu g) = 82 - 0.85\ t$ ($r = 0.966$; $P<10^{-5}$).

The decreases in C, N, H, and J during t followed an exponential pattern: $\ln y = b + mt$, where y is any measure for biomass (C, N, H in μg) or energy (J). To allow direct comparison, fitted curves were again converted to percentage values and shown in Figure 6 (only Z-1 stage as an example). For the other stages similar curves were obtained (Table 9). The slope parameters (= regression coefficients, m, in the log-transformed equations) were not statistically significantly different from each other. The b values were very close to the logarithms of the initial figures for biomass.

In all three larval instars the energy content (J/ind.) dropped more drastically than C, N, and H contents (Table 9). In the Z-1 there was also a slightly stronger decline in N as compared with C and H (Fig. 6). The maximal losses observed shortly before starvation death of the larvae were ca. 36 to 46% in the Z-1, 45 to 58% in the Z-2, and 43 to 51% in the megalopa.

TABLE 9.—Parameters of regression equations for loss of individual biomass in starved larval stages of *Hyas araneus*: $\ln y = b + mt$; t = time (d). For further explanation see Table 3.

Stage	*y*	*b*	*m*	*r*	df
Zoea I	C	3.127	−0.028	−0.986	61
Zoea 1	N	1.653	−0.032	−0.984	61
Zoea I	H	1.167	−0.027	−0.972	61
Zoea I	J	−0.285	−0.037	−0.981	61
Zoea II	C	4.082	−0.033	−0.868	25
Zoea II	N	2.548	−0.029	−0.836	25
Zoea II	H	2.166	−0.036	−0.843	25
Zoea II	J	0.698	−0.041	−0.886	25
Megalopa	C	4.663	−0.028	−0.634	32
Megalopa	N	3.181	−0.030	−0.673	32
Megalopa	H	2.748	−0.029	−0.608	32
Megalopa	J	1.268	−0.038	−0.698	32

The average daily energy loss per individual increased from the first to the last larval stage. If converted to weight-specific figures, a weak opposite trend became visible. This means that increasing reserves became available during the progress of development, and weight-specific metabolism tended to decrease somewhat. However, the above average values are only rough estimates, since the loss patterns are nonlinear (see above), but they do reflect general differences among stages (Table 10).

The decrease pattern in weight-specific energy contents of starved larvae (within stages) followed a hyperbola: $\ln J/mg\ DW = b + m \ln(t+1)$, where t = time (days), b is close to the logarithm of the initial value, and m is the slope.

TABLE 10.—Average daily energy loss in starved larval stages of *Hyas araneus* (estimated from carbon-hydrogen-nitrogen values). J = energy contents; DW = dry weight.

Stage	J/d per ind.	J/d per mg DW
Zoea I	0.02	0.35
Zoea II	0.07	0.32
Megalopa	0.11	0.28

The b values of the fitted curves were ca. 2.5, the m's were −0.20 (Z-2) to −0.23 (Z-1); and the r^2's varied between −0.964 ($P<0.002$; Z-2) and −0.992 ($P<10^{-10}$; Z-1).

Using the conversion factor 20.19 J/ml O_2 given by Brody (1945), approximate figures for oxygen consumption could be estimated from the energy values in Tables 6 to 8. In all stages there was apparently a drastic reduction in respiration rate during the first few days of starvation (Table 11). For comparison of the stages, again average values were computed (from values in Table 10). Corresponding to the weight-specific energy values (see above), from which they were derived, a weak decreasing trend became apparent (Table 11).

The C:N ratio (Fig. 5) did not follow a uniform pattern in starved larvae. In the Z-1 stage a long period of gradual increase was followed by a short period of rapid decrease. This suggests that protein was catabolized at a higher rate than other constituents during most of the starvation period; only in the premortal phase, were N-poor substances (most probably lipids) apparently used as the main energy source. In the Z-2 and in the megalopa variation was too high to discern clear trends. In the former instar the C:N ratio also showed a drop at the end suggesting some similarity with the Z-1, whereas in the latter stage apparently it did not change at all.

The C:H ratio was practically constant in all larval instars. It was in most cases significantly lower in fed than in starved larvae. The mean values and 95% confidence intervals (by weight) were 6.67±0.08 versus 7.07±0.012 in the Z-1 ($P<10^{-5}$), 6.64±0.26 versus 6.98±0.30 in the Z-2 (not significant), and 6.49±0.11 versus 6.80±0.28 in the megalopa ($P=0.014$). There was a similar statistically significant difference ($P = 0.002$) between the C:H ratios found in Z-1 larvae in May 1979 (6.86±0.09) and in February 1980 (6.67±0.08).

TABLE 11.—Weight-specific respiration rates (μl O_2/h per mg dry weight) in relation to the time of starvation of *Hyas araneus*.

Stage	Days of starvation				
	2	4	8	>8	$\bar{x}$[1]
Zoea I	3.6	0.7	0.3		0.73
Zoea II		1.6	0.4		0.66
Megalopa		2.3	0.5	0.2	0.59

[1]Computed from Table 10 data.

DISCUSSION

Larval growth has been measured and described in a number of different ways. Increments in zoeal body size obey the general rules summarized by Rice (1968), who calculated an average growth factor of 1.29 for brachyurans. From the figures given by Christiansen (1973) for *H. araneus*, factors of 1.26 to 1.30 can be derived, depending on the distance measured. A factor of 1.3 is also obtained, if size is assumed to be proportional to the cube root of DW. As pointed out by Rice (1968), the megalopa can hardly be included in those considerations because of its different shape.

It is generally accepted that FW is a poor measure of actual biomass. Its determination is inaccurate and thus yields highly variable results. Moreover, it does not change in an orderly manner during the molt cycle and therefore, it must be regarded as insensitive to changes in organic matter. This is caused by changes in the water content. It is difficult to understand why a number of authors described biochemical and physiological changes in developing crustacean larvae on a wet weight basis, and so severely reduced the value of their information. We suggest that FW or Formalin wet weight never be used as a reference base in such studies, but only as a source of additional information (e.g., for water content of tissues).

DW is a far better measure of biomass, although it is influenced by inorganic salts. Unfortunately, different drying methods (temperatures and times) are used by different investigators. Ash-free DW should improve the accuracy in physiological studies, if used as a basic unit. However, again drying and combustion temperatures and times are not uniformly applied.

Elemental composition, especially C content, can be used as a reliable expression of living organic substance. Inorganic C does not play a signficant role in marine planktonic organisms (Curl 1962) and therefore C is also a measure of energy equivalents (Salonen et al. 1976). C-based energy estimations apparently tend to be somewhat lower than those calculated from bio-

chemical composition (Anger and Nair 1979); comparison of both methods with direct calorimetry in identical material should be worthwhile. However, the J values given in this paper compare favorably with those reported elsewhere for decapod larvae (e.g., Cummins and Wuycheck 1971; Mootz and Epifanio 1974; Logan and Epifanio 1978; Capuzzo and Lancaster 1979; Dawirs 1980; Stephenson and Knight 1980).

The interpretation of changes in the relative chemical composition of larvae (C:N, C:H) leads to interesting assumptions about physiological processes, but there is a need for complementary biochemical investigations. Such analyses are planned for future studies as an extension of the present results. So far, our figures compare favorably with those given in the literature (Childress and Nygaard 1974; Ikeda 1974; Omori 1979; Dawirs 1980). Ikeda (1974) investigated a large number of zooplankton species, and he found that C:N (by weight) is in most cases 3 to 5, whereas C:H is mostly 6 to 7.

Growth (any measure except size and FW) during larval development in decapod crustacea usually follows—at least for some period—an exponential pattern, if gain from stage to stage is considered (Reeve 1969; Mootz and Epifanio 1974; Logan and Epifanio 1978; Johns and Pechenik 1980; Stephenson and Knight 1980). This also holds true for the zoeal stages of *Hyas araneus*. Interpolation of biomass values within single stages from such exponential curves yields poor correspondence of predicted and observed data, because growth within stages follows different patterns. In both zoeae it could be described most accurately by power functions, whereas exponential regressions do not fit as well. At the end of the molt cycle, however, such parabola-shaped fitted growth curves lose their applicability. This final period probably corresponds to the stages D_2 to D_4, during which molt is prepared by separating the epidermis from the old cuticle (Freeman and Costlow 1980). Possibly, there is no more significant food uptake during this phase of body reconstruction (Anger and Dawirs 1981).

In the megalopa, another growth pattern was found. The period of body reconstruction and of presumed inability to take up food preceding metamorphosis appears to be much longer in this stage. The daily energy loss per individual was three times higher during this time as opposed to megalopae starved from the beginning. This contrast suggests that a final fasting period is a normal part of the development program, not considered starvation, and thus not counterbalanced by reduced metabolism. This assumption is supported by a number of observations in other decapod megalopae (Mootz and Epifanio 1974; Schatzlein and Costlow 1978; Dawirs 1980; for recent review see Anger and Dawirs 1981).

The duration of the megalopa stage is much more variable than the zoeal instars. This fact may be related to the ecological role of the megalopa which is to select a biotope suitable for adult life. The capacity to delay selection should be related to the amount of reserve accumulated prior to the change in energy balance. This strategy is in contrast to that observed by Pechenik (1980) in gastropod larvae. These do not cease to grow with the onset of metamorphic competence, and their capability to delay metamorphosis appears to be related to the preceding growth rate. More detailed investigations on the nutritional and ecological needs of the megalopa stage are necessary for a better understanding of this critical phase in benthic recruitment.

All these complicated changes of biomass as well as their extent (two- to threefold increases within single stages) suggest that the use of "characteristic" values for particular instars applied in energy budgets and other energetic considerations must lead to very rough figures.

Another complicating factor is annual or seasonal variation in initial biomass of hatching larvae and in their growth rate. Since viability also appears to be related to this kind of variation, future studies will have to examine its degree and significance. The same holds true for possible systematic differences between laboratory-reared larvae and those obtained from wild plankton. Several authors (Knight 1970 and earlier papers; Rice and Provenzano 1970; Ingle and Rice 1971) observed higher growth rates in naturally grown developmental stages of different decapod species.

Only a small part of the organic matter accumulated during the zoeal stages is lost in exuviae. This is much different in the megalopa. More than three times more matter and energy was found in its cast exoskeleton than in both zoeae combined. These and other striking dissimilarities between zoea and megalopa larvae underline their different roles. The former accumulate energy-rich substances taken from the pelagic food web, and they are responsible for dispersal of the species. The latter stage, which

often crawls on the bottom, presumably will test suitable benthic habitats, before it goes through metamorphosis at a selected site. It appears that a rigid exoskeleton is advantageous as a protective means in the evolution of benthic crustaceans, whereas in pelagic species and stages it is probably disadvantageous for energetic reasons (increasing swimming energy).

The preliminary determinations of feeding rates on *Artemia sp.* nauplii yielded almost the same values (in C per day) as observed by Anger and Nair (1979) using *Polydora ciliata* larvae as prey. This confirms that the amounts in the above data are correct, but further studies considering the whole molt cycle in each larval stage will be necessary for comparisons with the growth measurements of the present investigation. The feeding rates observed in the Z-1 of *H. araneus* as well as larval DW are similar to those found by Mootz and Epifanio (1974) in the Z-4 stage of *Menippe mercenaria.*

Measuring the loss of organic matter and energy during starvation bears the same technical problems as measuring growth. FW, apart from its inaccuracy, is practically constant even during long-term starvation. This masking of changes in organic constituents is again caused by changes in water content. We assume that the underlying mechanism is some kind of starvation edema. Due to degradation of amino acids, the osmotic pressure in the hemolymph must decrease, and consequently water may passively enter body tissues. The water lost in the hemolymph might be replaced by seawater. This assumption would explain the observed net increase in body volume, water, and ash contents of starving larvae (Ikeda 1971, 1974; Mayzaud 1976). Instrusion of inorganic salts replacing degraded organic ions presumably is responsible not only for increasing ash portions, but also for the low degree of loss in DW. The latter observation means that DW can also be used in energetic studies of starving zooplankton to a limited degree, because it does not reflect actual losses in organic matter and energy.

Losses in C, N, H, and individual J's followed an exponential pattern with a weak curvature. The maximum possible losses until death amounted to ca. 40 to 60% of initial values, depending on the parameter and larval stage under consideration. These observations correspond to those by Anger and Nair (1979) and Dawirs (unpubl. data) on starved larvae of *H. araneus* and *Carcinus maenas*, respectively. Ikeda (1974) reported reductions in biomass of other zooplankton down to 20%. Our figures also become higher if chitin is excluded from these calculations.

Anger and Dawirs (1981) found that feeding after initial starvation in Z-1 larvae of *H. araneus* is successful only if a certain time (point-of-no-return, PNR) is not exceeded. Comparing this time span with the above biomass data, the actual limits of starvation resistance are already reached when 25 to 30% of organic matter (C,N,H) or 30 to 35% of individual energy are lost. Beyond this PNR another ca. 10% loss in all these parameters is possible, before the larva dies, regardless of eventual food availability. Fifty percent of the larvae already reach this limit (PNR_{50}) when only ca. 20% of the organic substance or ca. 25% of energy is lost. The PNR values for the other stages have not yet been determined.

Another finding reported by Anger and Dawirs (1981) is that relatively short initial feeding periods suffice for zoeae of *H. araneus* to successfully reach the next stage (Z-2 or megalopa), regardless of further food availability. Converting these time spans to biomass data, a surprising agreement in both zoeal stages is found: 50% of the larvae reach this "point-of-reserve-saturation" (PRS_{50}), when they have gained ca. 70% N, 90% C and H each, and ca. 95% energy (related to early postmolt levels). If food is continually available, considerable further accumulation of organic matter and energy will take place (see above), but this additional reserve will not be needed before the next stage is reached. If no prey is available during this period (presumably premolt) the next stage will be significantly prolonged, thus revealing a certain dependence on reserves accumulated during the preceding zoeal stage. Anger and Dawirs (1981) suggested that sterols (precursors of the molting hormone, ecdysterone) may play a crucial role in this phenomenon.

It is doubtful that energetics alone can explain the early appearance of the PNR, since the actual losses in organic body substance are rather low at that time. We assume that an irreversible damage in some hormonal or enzymatic system is involved in ecdysis.

The weight-specific metabolic rate is a major factor deciding the maximal survival time under starvation (Ikeda 1974). It is far lower in starved as compared with fed zooplankton (see, e.g., Ikeda 1977 and earlier papers cited therein;

Mayzaud 1976; Logan and Epifanio 1978; Capuzzo and Lancaster 1979). The hyperbola-shaped decrease pattern in weight-specific energy (see above) is in accordance with that described by Mayzaud (1976) for respiration rates in starved zooplankton. There is an initial acclimation period with strongly decreasing metabolic rate, followed by more or less constant values. Our estimates for oxygen consumption follow this pattern, and their amounts compare favorably with literature data, if starvation and relatively low temperature (12°C) are taken into account (for review see Schatzlein and Costlow 1978).

In a low temperature range, high Q_{10} values are to be expected. This assumption is confirmed by extremely long survival times observed by Anger and Dawirs (1981). These figures of starvation resistance as well as our calculations of weight-specific respiration rates fit the quantitative relationship between these two parameters described by Ikeda (1974).

The metabolism of starved *H. araneus* larvae is mainly based on protein degradation (Anger and Nair 1979). According to the literature, this is a general feature in crustaceans (e.g., Mayzaud 1976; Ikeda 1977 and earlier papers; Capuzzo and Lancaster 1979). Our observations on changes in the C:N ratio suggest that during the final (premortal) period of long-term starvation, lipids also become important as a last reserve. However, at this time the larva is already doomed to die, regardless of eventual food availability, since the PNR has been exceeded (Anger and Dawirs 1981).

The amount of reserve and proportions of metabolic pathways apparently are also subject to annual and seasonal variation, possibly even to differences among different parts of one brood (e.g., Regnault 1969; Pandian and Schumann 1967; Pandian 1970; Pandian and Katre 1972; Anger and Dawirs 1981). Those changes may also explain differences between daily energy losses in starved zoeae estimated by Anger and Nair (1979) and in the present study. Future investigations will have to examine the amount and significance of such natural variation superimposed on the response patterns of decapod larvae in different feeding conditons.

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A MULTISPECIES ANALYSIS OF THE COMMERCIAL DEEP-SEA HANDLINE FISHERY IN HAWAII

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ABSTRACT

In the Hawaiian Islands 13 species of bottom fish are commonly harvested in the commercial deep-sea handline fishery. These are all high-level carnivores, including snappers, jacks, and a species of grouper, which are sought in water depths ranging from 60 to 350 m. Cluster analyses performed on the Hawaii Division of Fish and Game commercial catch report data suggest the existence of three bottom fish species groups which apparently segregate on the basis of depth distribution. These groups seem to be stable through time and similar among differing geographic localities.

Two measures of fishing effort, catch-records and fisherman-days, were compared to determine which is more suitable for use in stock-production analyses. Fisherman-days was selected because, among other reasons, it repeatedly demonstrates a stronger negative correlation with catch per unit effort.

Application of the Schaefer stock-production model to this multispecies fishery on a species-by-species basis provides an inadequate description of productivity. When catch statistics are aggregated according to the three cluster analysis species groups the results are much improved. In this regard consistently significant results and production estimates were obtained from the Maui-Lanai-Kahoolawe-Molokai bank, a region which presently accounts for about half of the total Hawaii catch. No significant interaction among the cluster groups was detected. When all 13 bottom fish species are analyzed together, the results are in agreement with the preceding analysis. Examining the aggregation process suggests that the model based on the intermediate level of aggregation (cluster groups) explains slightly more of the variation in total catch than does the model which treats all 13 species together.

We estimate the annual maximum sustainable yield of the commercial deep-sea handline fishery around the Maui-Lanai-Kahoolawe-Molokai bank to be 106 metric tons or about 272 kg/nmi of 100-fathom isobath. Because recreational catch is unaccounted for these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this maximum-sustainable-yield level.

Effective management programs for tropical fisheries are difficult to achieve (Pauly 1979). Often attempts at managing these fisheries are based on the application of inappropriate models to sparse data. Both deficiencies are due in part to the multiplicity of fish species inhabiting tropical environments. This great diversity (Sale 1977; Talbot et al. 1979) makes it difficult to compile adequate data for all species of interest. The Hawaiian Islands, which straddle the Tropic of Cancer, possess a relatively impoverished tropical ichthyofauna, yet between 600 and 700 species are known from this region (Gosline and Brock 1960). Coupled with high diversity, many tropical countries lack a refined statistical system for the acquisition and storage of fisheries data. In concert these two limitations impose severe restrictions on the quantity and quality of data which are currently available for the analysis and management of tropical fisheries (Pope 1979). Furthermore, classical fisheries models thus far developed have been directed toward the management of temperate and boreal stocks (Food and Agriculture Organization of the United Nations (FAO) 1978). These models usually treat species as independent management units. It has become apparent that such an approach is often inadequate when extrapolated to the tropics where community dynamics become increasingly important (Pauly 1979).

The multispecies approach to managing fisheries exploitation in complex ecosystems has only recently acquired a substantive base in the literature. Early work by Larkin (1963, 1966)

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evaluated the consequences of Lotka-Volterra competition and predator-prey systems on optimum exploitation strategies. Paulik et al. (1967) examined the problem of maximizing the yield from a fishery composed of mixed stocks, each with a unique spawner-recruit curve. A large body of descriptive work has documented the successional nature of changing catch composition which is often characteristic of increasing exploitation in a multispecies fishery (e.g., Regier 1973). Several recent multispecies investigations present highly sophisticated ecosystem models that require numerical solution and/or dynamic simulation, as well as numerous parameter estimates (Parrish 1975; Andersen and Ursin 1977; Laevastu and Favorite 1978[3]).

An alternative to this latter approach simply treats multispecies fisheries as though they behave as would a single species stock and evaluates production by application of the total biomass Schaefer model (TBSM) (Pope 1979). Brown et al. (1976) estimated total finfish production in the northwest Atlantic in this manner, as did Brander (1977) for demersal fish and shellfish in the Irish Sea. A review of this approach shows that "these overall Schaefer models generally seem to fit the data rather better than the fits experienced with their component stocks" (FAO 1978). Among the possible reasons for this are 1) the TBSM really presents a more realistic representation of multispecies fisheries than does summing the yields of individual stocks, 2) the better fit results from some type of averaging process, 3) artifacts in the method of fitting and/or shifts in preference between species within a fishery may result in a better fit when total biomass is evaluated (FAO 1978; Pauly 1979; Pope 1979). Several authors have issued the caveat that a thorough understanding of trophic relations is fundamental to managing any multispecies fishery and that such considerations may easily invalidate the application of the TBSM (May et al. 1979; Pauly 1979).

This paper estimates the productivity of deep-dwelling bottom fish stocks around the main islands of the Hawaiian Archipelago using stock-production methods. The fishery for these stocks is conducted in offshore waters ranging in depth from 60 to 350 m where a variety of species, principally snappers of the Family Lutjanidae, abound. In addition to providing preliminary productivity estimates for this fishery, an examination of the performance of the TBSM at various levels of species aggregation is undertaken. This latter analysis provides a quasi-quantitative means of evaluating the applicability of the TBSM to the Hawaiian offshore handline fishery.

SOURCES OF DATA AND DESCRIPTION OF THE FISHERY

In the State of Hawaii, all fishermen who sell a portion of their catch must be licensed as commercial fishermen by the Hawaii Division of Fish and Game (HDFG). There is no licensing requirement for recreational fishing. New commercial licenses are issued every fiscal year and once licensed, fishermen are required to submit a monthly catch report whether or not they have fished. These monthly catch reports require from each fisherman entries on the days and areas in which he fished, the types of fishing gear used, the number of individuals and pounds of the different species landed, and the dollar value of the catch. Incomplete reporting is thought to be common and raises the question of bias in the data (Ralston 1979[4]). Perhaps more serious is the omission of any direct measure of fishing effort or fishing power in the information concerning bottom fish obtained from these reports.

Monthly catch reports are coded, keypunched, and stored on magnetic tape for future use by HDFG. These data are the basis of this study and currently span the 20-yr period 1959 to 1978 inclusive, comprising some 600,000 records. While the date are voluminous, the extent of nonreporting by recreational fishermen and of incomplete or underreporting by commercial fishermen is unknown.

The complete HDFG data account for all types of commercial fishing in the State of Hawaii; therefore, only those catch records which list deep-sea handline fishing gear were used in this study. This reduced the data to one-fourth its original size and defined the scope of the fishery. Although the name suggests otherwise, the fishing gear is primarily hydraulic or electric

[3]Laevastu, T., and F. Favorite. 1978. Numerical evaluation of marine ecosystems. Part 1. Deterministic bulk biomass model (BBM). NWAFC Process. Rep., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 22 p. (Unpubl. rep.)

[4]Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. (Unpubl. rep.)

although some manual equipment remains in use.

The fishery mainly exploits 13 categories of fish species (Table 1). Confusion concerning the taxonomy of species in the family Carangidae prohibits a more detailed classification of these forms although *Pseudocaranx dentex* and *Caranx ignobilis* probably account for the majority of ulua landed in Hawaii. While *P. dentex* is abundant in the Northwestern Hawaiian Islands, it is apparently uncommon around the main high islands (Uchida[5]). Further confusion is apt to result from the findings of Anderson (1981), who recently revised the genus *Etelis* and changed the names of both Hawaiian species. In addition, two hogfish species are frequently taken, *Bodianus bilunulatus* and *B. vulpinus*, although the former species seems to inhabit somewhat shallower depths than the latter. Of those species listed, most are caught almost exclusively with deep-sea handline gear. The exceptions are ta'ape, ulua, and a'awa which are commonly taken by several other methods (e.g., inshore handline, purse seine, gill net, etc.) (Ralston footnote 4). Catches of these species reported here include only those portions taken in the offshore handline fishery.

In descending order the dominant species in the fishery by weight are the opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala (Ralston footnote 4). These species taken together accounted for 86% of the total catch by weight in 1978, nearly all of which was marketed in Hawaii as fresh fish. Total landings from the fishery have remained relatively constant from 1959 to 1978, showing a slight increase in recent years, although higher catches were briefly reported during the late 1940's and early 1950's (Fig. 1) (Ralston footnote 4). Most of these species are highly prized and in recent years have averaged close to $5.00/kg ex-vessel.

In the past about 85% of the catch of deep dwelling bottom fish has been made around the main Hawaiian Islands in contrast to the uninhabited Northwestern Hawaiian Islands (Grigg and Pfund 1980). Catches from the latter area have increased remarkably in the last 2 yr, as larger, more seaworthy vessels have entered the fishery. Nonetheless, the lack of sufficient data

TABLE 1.—Principal species of fish landed in the Hawaiian offshore handline fishery.

Family	Species	Common name	Average weight (kg)
Lutjanidae	*Aphareus rutilans*	Lehi	3-8
	Aprion virescens	Uku	2-8
	Etelis coruscans	Onaga	2-8
	E. carbunculus	Ehu	0.5-2
	Lutjanus kasmira	Ta'ape	0.5
	Pristipomoides filamentosus	Opakapaka	1-6
	P. sieboldii	Kalekale	0.5
	P. zonatus	Gindai	0.5-2
Carangidae	*Caranx* and *Carangoides* spp.	Ulua	1-10
	Seriola dumerili	Kahala	3-10
Serranidae	*Epinephelus quernus*	Hapu'upu'u	3-10
Labridae	*Bodianus* spp.	A'awa	1-3
Scorpaenidae	*Pontinus macrocephala*	Nohu	1-2

[5]R. N. Uchida, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. November 1980.

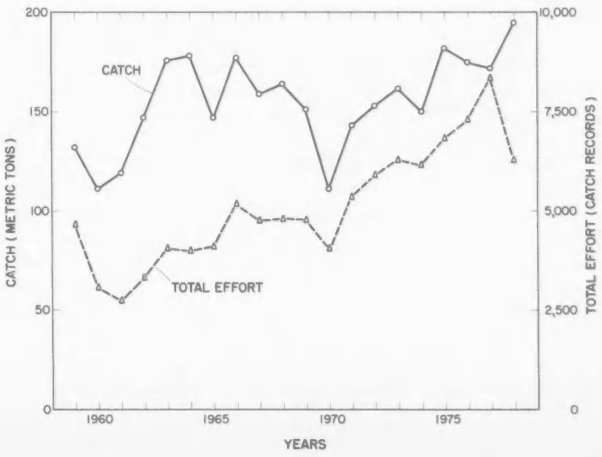

FIGURE 1.—Annual landings and total annual effort for the commercial deep-sea handline fishery in the main high islands of the Hawaiian Archipelago.

from this region prevents its analysis; the results presented here pertain only to the eight main islands of the archipelago (Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau, including Kaula Rock). Within this region fishing is conducted on offshore banks and pinnacles, primarily in the vicinity of the 100-fathom isobath. In the Hawaiian Islands the sea bottom typically extends away from shore at a depth of 30 fathoms for some distance and then falls abruptly to very great depths over a relatively short horizontal span (Brock and Chamberlain 1968). Most fishing occurs in this steep dropoff zone. Hence it is possible to crudely estimate the relative amount of total bottom fish habitat around a fishing bank by determining the length of the 100-fathom isobath surrounding it (Table 2). The maximum depth between the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM) is <100 fathoms; therefore, they were pooled and treated as a single bank (Fig. 2). All bottom fish taken from a bank were considered one stock because movements of juveniles and adults across deep water from one bank to the next are highly improbable whereas lateral movements around the perimeter of the 100-fathom isobath of a bank cannot be discounted. The Islands of Oahu and Hawaii are separated by deep water from all other islands and banks, hence, by definition, they harbor distinct stocks. Kauai, Niihau, and Kaula Rock (KNK), although separated across short distances by deep water, were analyzed together because they present a similar fishing profile and they are closely situated to one another. Thus, based on this classification four distinct stocks were analyzed independently. The extent of larval dispersal between these stocks is unknown at present but is currently under study (Shaklee[6]). A more detailed description of this fishery may be found in Ralston (footnote 4) or in Hawaii Department of Land and Natural Resources (1979).

TABLE 2.—A list of the four banks which harbor separately defined stocks. The length of the 100-fathom isobath around a bank roughly measures the extent of its bottom fish habitat.

Bank	Percent contribution to total landings	Approximate length of 100-fathom isobath (nmi)
Hawaii	21	290
MLKM[1]	56	390
Oahu	12	150
KNK[2]	11	195

[1]Maui-Lanai-Kahoolawe-Molokai.
[2]Kauai, Niihau, and Kaula Rock.

FISHING EFFORT

The ultimate goal of any stock-production analysis is to relate the impact of variable fishing pressure on stock abundance. Fishing pressure

[6]J. G. Shaklee, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744, pers. commun. 1979.

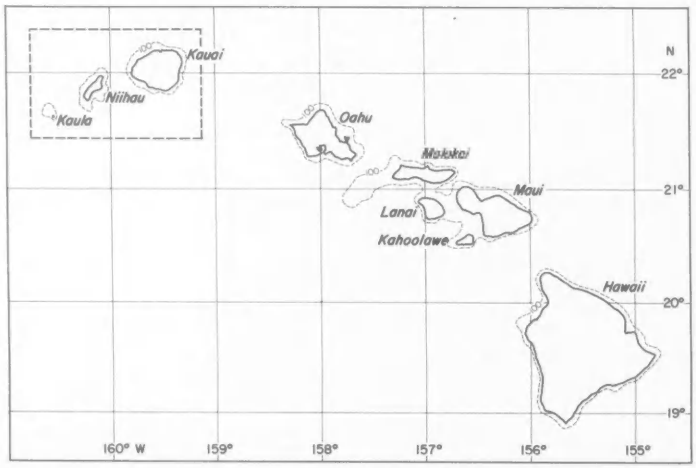

FIGURE 2.—Map of the eight main Hawaiian Islands and Kaula Rock with the 100-fathom isobath included.

is most conveniently formulated as instantaneous fishing mortality (F), measured over some arbitrary interval of time, usually 1 yr (Ricker 1975). Frequently it is not possible to measure F directly, however, and so a proportionate measure of F is selected, i.e., fishing effort or f. The ideal choice of units for fishing effort results in a linear correspondence between F and f, a zero intercept, and minimal residual variance (Rothschild 1977). Because F is frequently unknown, it is often difficult to ascertain whether these criteria are met and yet the selection of an appropriate measure of fishing effort is most critical to meeting the assumptions of a stock-production analysis. Ample consideration should be given to these factors before the data are collected.

No attempt has been made in the HDFG data to record either the fishing effort or the fishing power of individual fishermen. A suitable measure of fishing mortality in this fishery would be the cumulative number of hook-hours or line-hours of fishing. While such figures are currently unavailable, it has been possible to determine the total number of fishing records filed in a year which report the catch of a particular species. This statistic, the number of daily reports by fishermen who have caught any one particular species, was frequently computed and is termed catch-records. Figure 1 presents, in addition to the catch, the total number of deep-sea handline catch-records filed from 1959 to 1978 concerning all 13 species of bottom fish. This measure of fishing effort does not always correspond to the number of fisherman-days because one operator may catch several species during a single day of fishing. In this instance the reporting of each particular species comprises one catch-record. Thus, when aggregated species groups are considered, the number of fisherman-days will always be fewer than the total number of catch-records. When species are considered independently of one another the two figures are equal (catch-records = fisherman-days).

Interpreting the meaning of a fisherman-day as a unit of fishing effort in this fishery is difficult. It was tabulated by following the daily reports of individual fishermen, identified by their commercial fishing license numbers. All commercial fishermen in Hawaii, whether captain or crew, must have a license. It is likely that many catch reports are filed only by boat captains who document the landings of an entire fishing vessel, which may have a variable number of crew members. Thus a fisherman-day, as defined here, may reasonably be thought of as a vessel-day. However, because this unit of effort is defined and specified on the basis of commercial fishing licenses, in the interests of exactitude, we have chosen to use the term fisherman-day.

RESULTS

Clustering

The usual method of aggregating catch data would be to pool all 13 deep-sea handline species into a single group and to analyze the total with the TBSM. An alternative is to employ a multivariate statistical procedure to assess the degree of colinearity among species and to define species groups based on the strength of interspecies associations in the catch (Pope 1979). Such an approach would identify those bottom fish which tended to appear with one another in the catch to the exclusion of others and would measure the extent of correlation of fishing mortality among species. Pope (1979) has termed this "technological interaction" and has discussed its importance in multispecies fisheries. Separate application of the TBSM to each species group formed by clustering would constitute an analysis performed at an intermediate level of species aggregation. Conceptually this is desirable because in the Hawaiian offshore handline fishery different species are known to exhibit stratification by depth (Strasburg et al. 1968).

Cluster analyses were performed with a computer routine (Dixon 1977, program P1M) where the 13 species of bottom fish comprised the variables to be clustered and the catch from a single day's fishing formed one case. Associations were computed on the basis of the landed weight of each species. The average linkage between groups defined the criterion for amalgamating clusters and correlation coefficients were used as measures of similarity.

Separate analyses were performed for each of the four designated bank (Table 2) areas to assess whether obvious differences exist among banks with regard to interspecies associations. Similarly, separate analyses were conducted for the years 1959, 1965, 1971, and 1977 to see whether temporal variation in species grouping is an important factor to consider.

No striking differences or patterns emerged from these various comparisons. The intrinsic

variation apparent between clusters obtained from the same bank in 3 adjacent years (Hawaii in 1976, 1977, and 1978) was as great as the variation in clustering found between different banks and through longer periods of time. While there were a few suggestions of differences in the species composition of groups among the four banks, these were relatively minor and were ignored. Only one fairly consistent pattern of grouping was repeatedly exhibited across banks and through time, and this was confirmed by a single clustering of all the data pooled together. This pattern shows that the bottom fish fishery is loosely composed of three species groups which are apparently segregated on the basis of the depth range of member species (Table 3) (for depth distributions see Gosline and Brock 1960; Brock and Chamberlain 1968; Strasburg et al. 1968). These groups represent species assemblages which are for the most part independent of time and/or geographic location.

The delimitation of these three species groups is somewhat arbitrary and should not be viewed as the only way in which an intermediate level of species aggregation of the catch could be achieved. Nevertheless this grouping structure is reasonable and its use enhances the biological realism of the multispecies model by identifying and classifying those species which seem to share the greatest correlation in fishing mortalities. In addition the grouping structure allows an assessment of the effect aggregation has on the fit of data to a Schaefer stock-production analysis. A brief discussion of each of these groups is appropriate.

The appearance of ulua, ta'ape, and a'awa in the shallowest group (Group I) is consistent with the observation that these three species are frequently harvested with other types of fishing gear. Members of this group are often seen by scuba divers who venture below 30 m, although the vertical distribution of these species in the deep-sea handline fishery is centered around the 60 m terrace which circles much of the Hawaiian Islands (Brock and Chamberlain 1968). Because the name ulua refers to several different carangid species, one of which (*P. dentex*) is most often taken with members of Group II in deeper water, it is evident that some inaccuracies in the classification exist. This particular defect is not so much a result of the clustering process as it is a result of faulty data. Kahala, on the other hand, range widely (Gosline and Brock 1960) and are known from throughout the depth ranges of both Groups I and II and occur even shallower. Its position in Group II may simply reflect the relatively greater fishing pressure exerted in the 100-200 m depth range where other members of Group II, such as the opakapaka and hapu'upu'u, are centered. The deepest group (Group III) is particularly well defined and is composed of three lutjanid species, two of which are deepwater eteline red snappers.

TABLE 3.—Bottom fish species groupings defined by cluster analysis.

Group	Species	Approximate depth range (m)
I	Ulua, uku, ta'ape, a'awa	30-140
II	Opakapaka, hapu'upu'u, kahala, gindai, lehi, nohu	80-240
III	Onaga, ehu, kalekale	200-350

Fishing Effort

An attempt was made to evaluate the two measures of fishing effort, catch-records and fisherman-days, on the basis of their correlation with catch per unit of effort (CPUE). The Schaefer model predicts that plots of CPUE against effort should demonstrate a linear relationship with a negative slope if the production of the stock is described by the logistic growth curve (Ricker 1975). Such a prediction generates a one-tailed test of the hypothesis that $\rho \geq 0$ against the alternative hypothesis that $\rho < 0$ where ρ is the population correlation coefficient between CPUE and f. Even though a negative correlation between CPUE and effort is expected in a situation where catch and effort are completely unrelated random variables, the degree of spurious correlation due to this effect will be small if the main cause of variation in CPUE is varying stock abundance (Gulland 1974).

Correlations were computed between these two variables, using both measures of fishing effort for each species group-bank combination ($3 \times 4 = 12$). Additional correlations were computed for the total aggregated catch from each of the four banks ($1 \times 4 = 4$), resulting in 16 comparisons of the two measures of effort (Table 4). Comparisons which might be based on treating species as independent stocks are inappropriate here because the two measures of effort become equal in this limiting case. One means of evaluating the effectiveness of these two measures is to compare the signs of the correlation coefficients (r) and the magnitudes of the coefficients of determination (r^2) for each. It

TABLE 4.—Comparisons of correlations of CPUE and fishing effort (f) for two different measures of f. The total aggregate incorporates all 13 species.

		Unit of fishing effort			
		Catch-records		Fisherman-days	
Group	Bank[1]	r	r^2	r	r^2
I	Hawaii	−0.095	0.01	−0.128	0.02
	MLKM	−0.358	0.13	[2]−0.503	0.25
	Oahu	−0.153	0.02	−0.259	0.07
	KNK	−0.180	0.03	−0.111	0.01
II	Hawaii	−0.111	0.01	−0.120	0.01
	MLKM	−0.379	0.14	[2]−0.769	0.59
	Oahu	+0.285	0.08	+0.293	0.09
	KNK	+0.481	0.23	+0.237	0.06
III	Hawaii	−0.187	0.03	−0.015	0.00
	MLKM	−0.240	0.06	[2]−0.502	0.25
	Oahu	−0.362	0.13	[2]−0.390	0.15
	KNK	−0.308	0.09	[2]−0.395	0.16
	Total aggregate				
	Hawaii	−0.150	0.02	−0.334	0.11
	MLKM	[2]−0.463	0.21	[2]−0.878	0.77
	Oahu	[2]−0.465	0.22	[2]−0.521	0.27
	KNK	+0.395	0.16	−0.165	0.03

[1]MLKM = Maui-Lanai-Kahoolawe-Molokai
KNK= Kauai, Niihau, and Kaula Rock.
[2]Significant at $P = 0.05$ level, one-tailed test, df = 18.

is apparent that in 13 of the 16 possible comparisons, fisherman-days showed a stronger negative correlation with CPUE than did catch-records. Based on these results we conclude that fisherman-days predicts the behavior of CPUE more precisely than catch-records. Use of this measure also eliminates repeated counting of effort statistics when more than one species in a group is caught on a particular day and has greater intuitive appeal as well. For these reasons we conclude that fisherman-days is the best measure of fishing effort available at present. It is worth noting that these two different measures of effort are approximately linear in their relationship to one another, implying that the superiority of fisherman-days over catch-records as a measure of effort is probably due to a smaller residual variance of instantaneous fishing mortality (F) on the former statistic than on the latter.

Stock Production Analyses

In this section the Schaefer model is applied to the deep-sea handline data in which the catch is aggregated at three different levels. At the first level a single-species Schaefer model is fitted to each species separately. Next, the TBSM is fitted to each of the three species groups delimited by the cluster analysis. In the final section the total aggregated catch of all 13 species taken together is analyzed with the TBSM. Fisherman-days was used as the measure of fishing effort throughout, but equilibrium approximation (Gulland 1972) was not attempted because no information was available concerning the longevity of these species and a previous application of this method to the data had shown little improvement in the results (Ralston footnote 4).

When each species is treated independently there are 52 separate analyses (4 banks with 13 species each). In only two of these regressions of CPUE on f is the null hypothesis $\beta \geq 0$, where β is the slope of the regression, rejected in favor of the alternative hypothesis $\beta < 0$. Both involved the MLKM bank where opakapaka ($t = -2.91$, df = 18) and uku ($t = -1.82$, df = 18) demonstrated significant inverse regressions in which respectively, 32% and 16% of the total variation in CPUE were explained. The significance of these two regressions can easily be attributed to the Type I error and consequently nothing can be concluded from these results concerning the productivity of these fishes.

The fit of the TBSM to the data is much improved when the three species groups are considered. The model was applied to the HDFG data 12 times; once for each species group and bank combination. Significant results ($P = 0.05$, one-tailed test) were obtained in 5 of the 12 applications of the model (Table 5). The three analyses from the MLKM bank were significant in every case and those for Group III were significant in three out of the four regressions tested. The observation that the results from the remaining banks and species groups are not significant is not so disturbing because 56% of all bottom fish landings are harvested from the MLKM bank (Table 2). An estimate of the maximum sustainable yield (MSY) and optimum effort was then computed for each of the five significant combinations, as well as a standardized measure of productivity, calculated as the sustainable yield of bottom fish per nautical mile of 100-fathom isobath. Assuming logistic growth of the stocks the catchability coefficient was estimated using the computer program PRODFIT (Fox 1975). The t value in the table refers to the test of the null hypothesis that the slope of a regression is zero or positive.

Pope (1979) has proposed an interactive model to describe multispecies fisheries in which total yield is depicted as the sum of the yields of individual species with additional terms to account for community interactions. In the simple two-species case the equation describing surplus production (Y) is:

TABLE 5.—Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where species have been aggregated according to cluster analysis species groupings.

Bank[1]	Species group	MSY[2] (kg/yr)	Optimum effort (fisherman-days)	MSY/nmi 100-fathom isobath	Catchability coefficient	*t* value (df = 18)
MLKM	I	23,000	480	60	0.00180	−2.47
	II	48,800	662	125	0.00062	−5.11
	III	31,900	396	82	0.00120	−2.46
Oahu	III	1,900	119	12	0.00280	−1.74
KNK	III	4,800	84	25	0.00600	−1.77

[1]MLKM = Maui-Lanai-Kahoolawe-Molokai
KNK = Kauai, Niihau, and Kaula Rock.
[2]MSY = maximum sustainable yield.

$$Y = a_1N_1 + a_2N_2 - b_1N_1^2 - b_2N_2^2 + (c_1 + c_2)N_1N_2 \quad (1)$$

where N_1 and N_2 refer to the population sizes of species one and two and a_1, a_2, b_1, b_2, c_1, and c_2 are model parameters (Pope 1979). This model is the sum of two single-species surplus production models with the additional term $(c_1 + c_2)N_1N_2$ to account for the interaction between the two species. Depending upon the signs of c_1 and c_2 the equation models predation, competition, or mutualism. More importantly, the sum of these two parameters determines the impact of the interaction on the sustainable yield of the system.

The question of whether significant interaction occurs among the cluster-analysis species groups was examined by considering the MLKM bank alone. The regressions of all three cluster groups were highly significant from this region and further treatment of these data is therefore considered appropriate.

In the three-species version of Equation (1) there are three terms involving the sum of c parameters. In this analysis a species group (I, II, or III) is treated as though it were a single species and the a and b parameters necessary to evaluate the equation were taken from the independently calculated regressions of Table 5. A nonlinear regression routine (SAS Institute 1979, program NLIN) was employed to estimate the sums of the various c parameters for the MLKM bank (Table 6). It is apparent that these sums do not differ significantly from zero and hence there is no evidence for significant interaction among groups. This result further supports the classification of species into independent assemblages for use in an aggregated treatment of the data.

In the final analysis all species were treated as a single group and the TBSM was applied to the total aggregate. Of the four possible regressions of CPUE on f, both the MLKM and Oahu banks yielded significant results (Table 7). Similar computations were performed for these sites as had been done previously. In addition the regression of total bottom fish CPUE on f for the MLKM bank and the corresponding catch curve (catch versus effort) were plotted (Fig. 3). It is reassuring to note that the sum of the three-species group MSY's from this bank, calculated from the preceding analysis, amounts to 103,700 kg/yr. This estimate compares favorably with the present result (a difference of about 2%) though the two figures were computed somewhat independently. A comparison of MSY/nmi 100-fathom isobath between these two banks reveals the Oahu value to be substantially less than the MLKM value. Although this may in actuality represent differences in habitat quality and productivity between these banks, there is the possibility that the difference is at least partially due to a difference in the extent of unreported recreational fishing pressure between the banks.

The results of the stock-production analysis for the MLKM bank provide statistically acceptable regressions, yet the estimates of production are

TABLE 6.—Tests of whether interaction between cluster analysis species groups have a significant effect on total bottom fish yield from the Maui-Lanai-Kahoolawe-Molokai bank.

Term	Parameters	Evaluated value	95% confidence limits
$(c_1 + c_2)\ N_1N_2$	$(c_1 + c_2)$	0.242	(−0.244, 0.728)
$(c_2 + c_3)\ N_2N_3$	$(c_2 + c_3)$	0.185	(−0.284, 0.654)
$(c_1 + c_3)\ N_1N_3$	$(c_1 + c_3)$	−0.868	(−2.365, 0.629)

TABLE 7.—Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where all species have been grouped into one total aggregate.

	Bank	
	MLKM[1]	Oahu
MSY[2] (kg/yr)	106,000	15,700
Optimum effort (fisherman-days)	901	424
MSY/nmi, 100-fathom isobath	272	105
Catchability coefficient	0.00080	0.00168
t value (df = 18)	−7.77	−2.59

[1]MLKM = Maui-Lanai-Kahoolawe-Molokai.
[2]MSY = maximum sustainable yield.

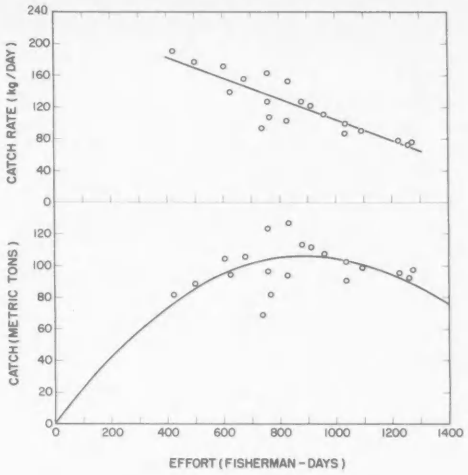

FIGURE 3.—Fitted production curves of CPUE and catch on fishing effort for the total aggregate landings of commercial bottom fish species from the Maui-Lanai-Kahoolawe-Molokai bank.

probably low. The HDFG data provide information on only a portion of the harvest of these species. Recreational bottom fishing is very popular around the main islands of the Hawaiian Archipelago but its relative impact is completely unknown. Furthermore, underreporting by commercial fishermen is also likely but its extent is hard to determine. Based on these considerations, the overall estimate of annual production calculated for the MLKM bank (272 kg bottom fish/nmi 100-fathom isobath) is best considered a lower bound for the surplus production obtainable from this type of fishery. In spite of the difficulty in determining precise estimates of productivity it would appear that the added effects of commercial and recreational fishing are close to fully exploiting the fishery (Fig. 3). In 1978 over 96 t (metric tons) of bottom fish were harvested from the MLKM bank by commercial fishermen.

DISCUSSION

Fishing Effort

One of the primary goals of this study has been to estimate the commercial productivity of Hawaii's offshore bottom fish resources. We have met with mixed success in our attempt because only one of the four study banks (Fig. 2) consistently provided significant results. In spite of this difficulty the MLKM is the largest of the four, producing well over half the total catch of bottom fish. The lack of statistical significance from the remaining banks may be due to several factors.

The impact of fishing is measured by correlating changes in fishing effort with catch rate (CPUE). If the observed range of fishing effort is too small to render an appreciable change in stock density then the impact of fishing cannot be measured. This hypothesis of insufficient variation in fishing mortality does not explain the lack of correlation between CPUE and effort from the Hawaii, Oahu, and KNK banks, however. The range in fishing intensity (defined as fisherman-days/nmi 100-fathom isobath or fishing effort per unit area) between the period 1959 and 1978 was the least for the MLKM bank where only a threefold difference in intensity was experienced. In contrast, fishing intensities ranged upwards from 4-fold (KNK) to 26-fold (Oahu) among the remaining banks. The range of fishing intensity to which the MLKM bank has been exposed is the least of all four sites and from this observation it would be reasonable to assume that all banks have experienced substantial variation in fishing mortality.

This follows logically only if the catchability coefficients for all banks are similar. It is probable, however, that these four regions differ with respect to the impact of one unit of fishing effort on the various stocks. If differences in fishable area are corrected for, a fisherman-day recorded from Oahu may well represent less fishing mortality than the same figure from the MLKM bank. In this regard, preliminary analyses based on fishing intensity rather than fishing effort showed that significant differences exist among the four banks in the relationship of CPUE to fishing intensity, precluding the option of pooling the data across banks (see Munro 1978 for a production analysis based on fishing intensity). In principle then, differences in catchability could explain the poor results from Hawaii, Oahu, and KNK if the catchability coefficient equating fisherman-days to fishing mortality from these areas is substantially less than that for MLKM. Variation in the extent of unreported catch among banks could compound this effect.

Other factors which remain unaccounted for

could further confound the interpretation of effort statistics. It is unknown whether the percentage of reported catch to total catch, among both commercial and recreational fishermen, is increasing, decreasing, or remaining stable. There has also been a trend toward increased fishing power with the advent of mechanical line haulers, but the exact amount of this effect is unknown. Considerations such as these make it difficult to quantify bottom fish effort statistics.

This brief discussion underscores the importance of employing an appropriate measure of fishing effort in which catchability does not vary according to the activities of man. It was possible to demonstrate the superiority of fisherman-days over catch records and yet the former measure proved to be inadequate when pooling across banks was attempted.

Effects of Aggregation

Investigators have reported that in a multispecies fishery the TBSM when applied to aggregated data often fits better than the Schaefer model applied on a species-by-species basis (FAO 1978; Pauly 1979; Pope 1979). We will examine this phenomenon for data from the MLKM bank for two levels of aggregation.

As shown in the results section we have applied the Schaefer model to CPUE and effort data at three levels of data aggregation. First we applied the Schaefer model to the data on a species-by-species basis. Then species were partitioned into three cluster groups, the catch and effort data were computed for each group, and the TBSM was fitted to each group. Finally all species were pooled into one group and the aggregate data consisting of total catch and effort were computed and fitted with the TBSM.

The fit of the TBSM to each of the three species groups and to the total group resulted in significant regressions for the MLKM bank while only 2 out of 13 single-species regressions for this bank were significant. This result may be due to the fact that the fishery exploits groups of species simultaneously and that our measure of fishing effort measures exploitation on species groups rather than single species. It is apparent that when the data in this study were progressively pooled, the correlation coefficients describing the fit became increasingly negative (Fig. 4). This result alone would suggest that aggregation led to a better fit. Unfortunately because only 2 out of the 13 single-species regressions were signficant, it is not appropriate to use the single-species results in our comparison of the effects of aggregation. Table 4 presents the correlation coefficients between CPUE and effort for each of the three cluster groups and the total aggregate. At first glance it appears that for the MLKM bank the TBSM applied to the total group fits substantially better ($r^2 = 0.77$ for fisherman-days) than the TBSM applied to any of the three species groups ($r^2 = 0.25$, $r^2 = 0.59$, and $r^2 = 0.25$). However, an examination of the correlations between fishing effort for the three cluster groups reveals that these variables are highly correlated (Table 8). Grunfeld and Griliches (1960) have cogently argued that increased colinearity of independent variables can lead to an increase in the goodness of fit (r^2) when data have been aggregated. This deceptive gain in the explanatory power of an aggregated independent variable prevents a direct compari-

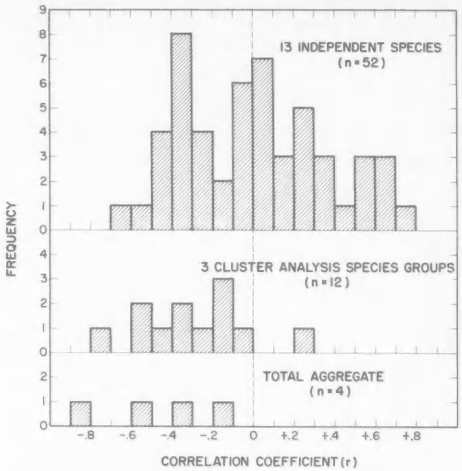

FIGURE 4.—Frequency distributions of correlation of coefficients between CPUE and fishing effort based on three levels of species aggregation.

TABLE 8.—Correlations of fishing effort (fisherman-days) (*f*) among cluster analysis species groups.

Group effort	*f*1	*f*2	*f*3
*f*1	1.000	0.943**	0.900**
*f*2	—	1.000	0.940**
*f*3	—	—	1.000

**Significant $P = 0.01$, df =78.

son of the coefficients of determination obtained from different levels of grouping. Thus it is improper to compare the goodness of fit for the grouped analysis to that for the total aggregate without correcting for this bias. They suggest that a more appropriate and direct way of comparing the effect of these two levels is to compare the proportion of variance in the total catch explained by the predicted total catch from the two levels of aggregation. We must use catch rather than CPUE as the dependent variable because the sum of the CPUE values predicted from each of the grouped models will not predict total CPUE.

When annual catch (C) rather than CPUE is used the Schaefer model becomes

$$C = af - bf^2 + E \tag{2}$$

where a and b are constants, f is fishing effort in fisherman-days, and E is a normal random variable with mean 0 and finite variance. In the case when catch and effort are aggregated into the three species groups there will be three equations of the form of Equation (2) based on the grouped annual catch (C_i) and grouped annual effort (f_i) for $i = 1, 2, 3$. For the completely aggregated TBSM there will be a single equation of the form of Equation (2) with total annual catch (TC) and total annual effort (Tf). In all four equations the nonlinear regression coefficients a and b can be estimated with the 20 yr of annual data from 1959 to 1978. We can then use these coefficients to obtain predicted group annual catches ($\hat{C}_{ij}$) for groups $i = 1, 2, 3$ and years $j = 1, 2, ..., 20$, and the predicted total annual catches (TC_j) for years $j = 1, 2, ..., 20$ given the corresponding effort statistics.

We now have two estimates of total annual catch based on either $\hat{TC}_j$ from the fully aggregated TBSM or $\hat{C}_{1j} + \hat{C}_{2j} + \hat{C}_{3j}$ from the three species groups regressions. We can compare these two levels of aggregation based on their accuracy in predicting TC. This is done by defining SS_g to be the sum of squares of $TC_j - \hat{C}_{1j} - \hat{C}_{2j} - \hat{C}_{3j}$ for $j = 1, 2, ..., 20$, or the deviations of the grouped predicted catch from the observed total, and defining $s_g^2 = SS_g/19$. Let SS_t be the sum of squares of $TC_j - \hat{TC}_j$, $j = 1, 2, ..., 20$, or the deviations of the predicted total catch of the completely aggregated TBSM from the observed total catch. Finally let $s_t^2 = SS_t/19$ and s_{TC}^2 be the sample variance of the total annual catch. Then the proportion of the variance of the total annual catch explained by the sum of the three species groups model is r_g^2 defined as:

$$r_g^2 = 1 - s_g^2/s_{TC}^2 \tag{3}$$

and the proportion of the variance in the total annual catch explained by the TBSM is r_t^2 defined as:

$$r_t^2 = 1 - s_t^2/s_{TC}^2 . \tag{4}$$

For the MLKM bank we determine $r_t^2 = 0.14$ and $r_g^2 = 0.18$. Thus the increased level of data aggregation going from treating the fishery as three separate groups to one total group does not in fact improve the fit of the catch curve although this appeared to be the case when the r^2 for the TBSM applied to the total group was compared to the r^2 values for the TBSM applied to each of the three cluster groups (Table 4, Fig. 4). As outlined previously these coefficients of determination, as calculated above, refer to the prediction of catch from effort data, for which the fit is substantially poorer than the fit of CPUE on effort.

A consideration of statistical aggregation theory has shown that the classification of bottom fish species into cluster groups results in slightly better predictions of total bottom fish catch than does analysis of the total aggregate. Since superior performance is achieved at an intermediate level of aggregation, it is possible to discount the undesirable effects of "averaging" which have troubled previous investigators (FAO 1978; Pauly 1979; Pope 1979). Furthermore, the lack of significant interaction among the species groups (Table 6) suggests that this particular application of the TBSM to the Hawaiian offshore handline fishery is appropriate.

Even though the separation of data from the MLKM bank into three species groups produced only a marginally better fit than the total aggregate model and the extra computations which are necessary were extensive (e.g., clustering), some advantage can be gained by splitting the fishery up into the groups listed in Table 3. Not only is the biological realism of the stock-production analysis enhanced but interesting patterns are also allowed to emerge. Notice, for example, that while the estimate of MSY for Group I from the MLKM bank is less than that for Group III from the same bank (Table 5), the fishing effort required to reach that figure is

substantially greater, in spite of the fact that the catchability coefficient for Group I is greater than for Group III. This apparent contradiction can be understood when estimates of carrying capacity and instantaneous growth rate are computed for the two groups. Ricker (1975) showed that the virgin shock biomass (B_∞) is equal to a/q and the intrinsic rate of natural increase (r) is equal to aq/b, where q is the catchability coefficient and a and b are the intercept and slope, respectively, of the regression of CPUE on effort. Using these equations the estimate of virgin biomass for Group I at the bank is much less than for Group III whereas the intrinsic rate of natural increase for Group I is nearly double that of Group III, hence, the disparity in catchability coefficients. This manner of evaluating the growth dynamics of the fishery implies that if fishing were to stop abruptly, Group I would recover to pristine levels much sooner than either Group II or III. Thus, this analysis would predict that a form of succession would occur around the MLKM bank if fishing were curtailed as a new equilibrium point was approached. Although there is little hope of manipulating the system to test this particular prediction of the model, this type of heuristic calculation can provide valuable insights concerning the consequences of different management programs.

Pope (1979) has shown that in a multispecies fishery an increase in the colinearity of effort values among species or groups will result in a more parabolic-shaped yield curve. Consequently, he argues that if fishing pressure is exerted in such a way that the fishing mortalities of the various species remain in constant ratio to one another, then the use of the TBSM is a realistic management option. He points out though, that it cannot be concluded that an MSY estimated by application of the model to actual data is anywhere near the global maximum of the system. These considerations bear directly on this study because of the high correlations of fishing effort among the three species groups. Even though MSY from the MLKM bank is estimated to be 106 t/yr it is quite possible that a substantially larger yield could be sustained if it were possible to alter the ratios of fishing mortality among the species groups. This possibility is not unrealistic because these groups seem to be for the most part spatially separated. In principle then, appropriate management action could reduce fishing effort on one group while simultaneously increasing that on another, but at present it is impossible to speculate about what the global MSY of the MLKM bank might be.

One of the least realistic aspects of the TBSM is its inability to adequately model trophic dynamics (Pauly 1979). The addition of Lotka-Volterra interaction terms to the model (Pope 1979) is a relatively simplistic attempt to deal with this problem. Pauly (1979) argued that the surplus-yield of fish predator-prey systems may be overestimated by the TBSM because of "prudent predation" by top carnivores. This theory (Slobodkin 1961) would propose that fish predators optimally harvest their fish prey, leaving little or no remaining latent productivity of the prey species for man to utilize. These arguments must impose group selectionist reasoning and suffer as a result. Nevertheless, the TBSM assumes that total stock size is greatest in a virgin state, a condition which need not be satisfied if limitation is internally imposed (May et al. 1979).

Fortunately these considerations do not detract from the value of the present analysis. The six dominant species in the fishery (opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala) are all high-level carnivores and occupy a similar trophic position. No predator-prey relationship is known to exist between any of the 13 species listed in Table 1, although extensive gut content analyses of all life history stages are currently unavailable. Thus, some of the objectionable aspects of the TBSM have been minimized by not including species from different trophic levels within the same analysis. Predator-prey relationships in a fisheries context are poorly understood at present and will probably require a more dynamic construct than the TBSM is capable of offering (May et al. 1979; Pauly 1979).

SUMMARY

Examining the HDFG catch report data shows that the commercial deep-sea handline fishery in the Hawaiian Islands is a multispecies fishery composed principally of 13 species of bottom fish, 6 of which comprise 86% of total landings. Snappers (Lutjanidae), jacks (Carangidae), and a species of grouper (Serranidae) dominate the catch, all of which are high-level carnivores.

In the main high islands of the Hawaiian Archipelago (see Figure 2) three bottom fish

species groups are recognized based on cluster analyses which measure the tendencies of the various species to appear with one ar. ıther in the catch. These groups seem to segregate on the basis of depth distribution, providing convenient biological assemblages for aggregating catch statistics.

Application of the Schaefer stock-production model to this fishery on a species-by-species basis provides an inadequate description of productivity. When species are aggregated into the cluster groups and analyzed with TBSM, the results are much improved. In this regard consistently significant results and production estimates were obtained from the MLKM bank, a region which presently accounts for half of the State of Hawaii's catch. No significant interaction among these groups was detected. When all 13 species are analyzed together, the results are in agreement with the preceding analysis. Based on TBSM applied to the MLKM bank, we estimate the annual MSY of the commercial deep-sea handline fishery to be 106 t or about 272 kg/nmi of 100-fathom isobath. Because recreational catch is unaccounted for, these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this MSY level.

By examining the effect of aggregating catch statistics we show that the production models based on the intermediate level of catch aggregation (cluster groups) together explain slightly more of the variation in the total catch than does the production model based on the total aggregate catch in spite of a higher coefficient of determination resulting from the latter analysis. High correlations of fishing effort among cluster groups account for this nonintuitive result.

Application of the Schaefer stock-production model to catch and effort data aggregated over species can be a useful tool for the analysis of a multispecies fishery. The appropriate level of aggregation will depend on biological and geographic factors.

ACKNOWLEDGMENTS

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DEVELOPMENT AND APPLICATION OF AN OBJECTIVE METHOD FOR CLASSIFYING LONG-FINNED SQUID, *LOLIGO PEALEI*, INTO SEXUAL MATURITY STAGES

WILLIAM K. MACY III[1]

ABSTRACT

An objective method of classifying long-finned squid, *Loligo pealei*, by their sexual maturity was developed using cluster and discriminant analysis techniques. The resulting system recognizes four developmental stages and employs a maximum of only five easily measured morphometric parameters. Such a system is easy to use and is suitable for large-scale field studies with relatively untrained help. The value of determining clearly recognized reproductive stages is demonstrated by an application of the method.

Each summer schools of long-finned squid, *Loligo pealei* Lesueur, 1821, move into shallow coastal waters from Delaware Bay to Cape Cod to spawn (Verrill 1882; Haefner 1964; Summers 1968, 1971). During the colder months, however, the squid are found only offshore, concentrated in canyon mouths along the continental slope (Summers 1967, 1969; Vovk and Nigmatullin 1972; Serchuk and Rathjen 1974). While the size/age composition of the species has been relatively well described by Verrill (1882), Summers (1967, 1968, 1969, 1971), Tibbetts (1975, 1977), and Mesnil (1977), many details of its reproductive cycle, particularly during the offshore period, remain unclear (see Summers 1969, 1971; Vovk 1972; Arnold and Williams-Arnold 1977; Mesnil 1977). From such studies it appears that *L. pealei* lives only 12-18 mo on average, and that like most squid it dies after spawning (Arnold and Williams-Arnold 1977). Details of the reproductive biology and population structure of such a short-lived species, with only two year classes at most, are especially important in the development of prudent stock management programs. Unfortunately, no single method for characterizing the reproductive state of individuals of this species has been employed to date.

A number of classification methods have been employed for a variety of squid species, which reflect both interspecific differences and differing requirements of the investigators using them (Tinbergen and Verwey 1945; Mangold-Wirz 1963; Fields 1965; Hayashi 1970; Vovk 1972; Holme 1974; Ikehara et al. 1977; Durward et al. 1978; Juanicó 1979; Hixon 1980). Many of these methods are slow because of the large number of variables required or the need for sample weighing or microscopic examination. Some methods also rely mainly on subjective distinctions.

From 1975 through 1978, ecological studies concerning the population structure, movement patterns, and feeding habits of *L. pealei* were conducted (Macy 1980). During the first year of the study, the Vovk (1972) method for classifying squid into one of five stages of sexual maturity was used with length-frequency data to characterize changes in the population reproductive structure over time. While the Vovk method was useful, in practice squid were often encountered which could not be readily classified. This report concerns the development and application of a new, faster, and more objective maturity classification system. The method was then successfully employed to classify large numbers of squid throughout the remainder of the study referred to above.

METHODS

From late April through November each year, squid were collected on an approximately biweekly basis throughout the inshore study area located in the southern part of the West Passage of Narragansett Bay, R.I. (inset Fig. 1). A balloon-type otter trawl (Oviatt and Nixon 1973), towed at ca. 4.6 km/h, was used. To insure randomness and adequate size-class representation, samples of at least 100 squid each were randomly selected from the pooled catch of duplicate 20-

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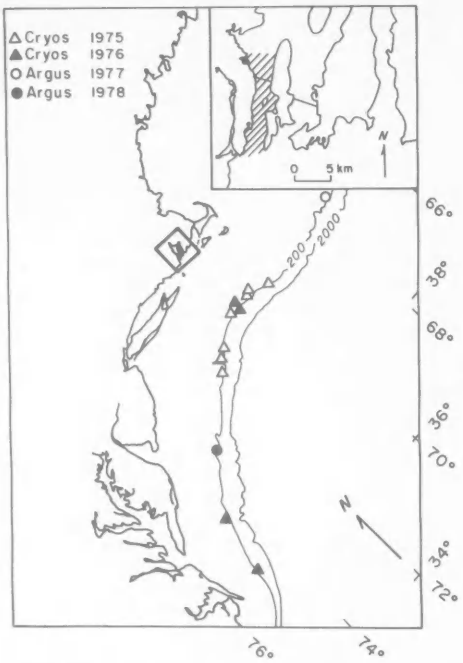


FIGURE 1.—Inshore and offshore sampling locations on the coast and continental shelf of New England. The study area in lower Narragansett Bay is indicated by shading in the inset. Depths in meters.

min trawl tows. The selected squid were bagged and placed in chilled containers for transportation to the laboratory, where they were either immediately examined or were quick-frozen at −25°C for storage. Additional frozen samples of 100-500 squid each were obtained from the National Marine Fisheries Service, Woods Hole, Mass.; from offshore surveys by the French vessel *Cryos* conducted during November-December 1975 and 1976; and from the Russian vessel *Argus* during November 1977 and March 1978 (Fig. 1). Only the 1976 Narragansett Bay and *Cryos* samples were used to develop and verify the classification system described here. The new system was then used to classify the 1977 and 1978 samples.

For analysis, squid were opened midventrally to expose internal organs and allow sexing. Twenty characters were then determined (Table 1). Length measurements were made to the nearest millimeter using a ruler along the greatest dimension, taking care not to stretch the organ or tissue. Frequently, the length of typical spermatophores can be determined while still within Needham's sac or the penis. Mantle width (MW, Table 1), a measure of mantle circumference, was defined as the distance across the widest part of the mantle when opened flat to form a rough isosceles triangle. Mantle thickness (MT) was measured at the thickest portion along the midventral incision. All weight measurements were blotted fresh or live weights (e.g., wet weight, WW, and gonad weight, GW) and were recorded to the nearest 0.01 g if <120 g or to the nearest 0.1 g if >120 g, on a top-loading digital balance. The relative abundance of spermatophores in Needham's sac (ASN), in the penis (ASP), of eggs in the ovary (AEO), or in the oviduct (AEOV) were scored on the basis of "none," "a few," or "many" present. In females, a distinction was also made between immature and mature eggs (Table 1). The four variables—ASN, ASP, AEO, and AEOV— were purposely scored on this nonquantitative basis to avoid time-consuming enumeration. After completing the above length measurements and abundance estimates, the complete reproductive tracts, including gonadal products (Table 1), were dissected out and weighed (GW). From the tabulated raw data the various proportional indices (GI, MWI, MTI, TLI, SPI, NGI, and AGI (see Table 1)) were then computed.

TABLE 1.—The initial 20 input parameters tested for classifying squid into maturity stages. See Figure 3 for organ identification.

Mantle length, cm = DML = dorsal mantle length
Wet weight, g = WW = total live weight
Mantle width, cm = MW
Mantle thickness, cm = MT
Gonad weight, g = GW[1]
Gonad index = GW/WW = GI
Mantle width index = MW/DML = MWI
Mantle thickness index = MT/DML = MTI
Males:
Testis length, cm = TL
Spermatophore length, cm = SPL[2]
Abundance of spermatophores in Needham's sac = ASN[3]
Abundance of spermatophores in penis = ASP[3]
Testis length index = TL/DML = TLI
Spermatophore length index = SPL/DML = SPI
Females:
Nidamental gland length, cm = NGL
Accessory gland length, cm = AGL
Abundance of eggs in ovary = AEO[4]
Abundance of eggs in oviduct = AEOV[3]
Nidamental gland index = NGL/DML = NGI
Accessory gland index = AGI/DML = AGI

[1]For females: (nidamental + accessory + oviducal glands) + ovary/oviduct + eggs.
For males: testis + (Needham's sac + spermatophoric organ + penis).
[2]Length of an average spermatophore excluding tail (= cap thread), scored as "0" if not present or if visible only as a round speck.
[3]Scored on a 1-3 scale, where 1 = none, 2 = "a few," 3 = abundant.
[4]Scored on a 1-5 scale, where 1 = none, 2 = "a few" immature, 3 = many immature, 4 = "a few" mature, 5 = many mature.

Statistical analyses were performed using the Biomed Computer Programs P-Series (BMDP) (Brown 1977) on an Itel AS-5^R computer[2] of the University of Rhode Island Academic Computer Center. The initial data matrix consisted of the 20 variables listed in Table 1, from 675 males and 693 females randomly selected from the 1976 *Cryos* offshore and 1976 Narragansett Bay inshore samples. After standardization of the variables, principal components analysis (BMDP program 4M) (Morrison 1976) was employed to group variables and to determine their importance in accounting for observed variance. Cluster analysis (BMDP 2M) was then used with the Euclidean-distance metric as the amalgamation algorithm to group cases (Anderberg 1973). Finally, stepwise linear discriminant analysis (BMDP 7M) (Anderson 1958) was used with different variable combinations to generate a series of functions which best discriminated between the groups identified in the cluster-analysis stage. A goal of 95% or better overall correct classification of individuals was set.

RESULTS

Development of the Discriminant Functions

The initial cluster analysis revealed only two major groupings for each sex. Further examination, however, suggested that the major clusters consisted of different size-based groupings of mature and immature individuals. Spent squid (using the Vovk (1972) scale) did not group together. Weight variables—WW, GW, and GI (Table 1)—were then dropped from the data matrix because it was known that length measures correlate well with their respective weight counterparts and because principal components analysis had not indicated any particular advantage to using one variable type or the other. Cluster analysis was then rerun using the remaining 17 variables. Four clusters of developmental stages could then be recognized, corresponding to "ripe/spent," "nearly mature," "advanced immature," and "immature" (barely sexable). Several size-based subgroups were still evident within the major clusters. After scoring the squid on a 1-4 scale based on the cluster results, subsequent discriminant analysis produced moderately good separation of the four groups.

Efforts were then focused on improving class separation and reducing the number of variables required. First, those cases which were suspected to be misclassified based on posterior probability and Mahalanobis D^2 statistics (Lachenbruch and Mickey 1968) were corrected. By this time a rather clear picture of the characteristics of each stage had been formed, and thus inspection of the raw data was often sufficient to determine if reclassification was warranted. Using different combinations of variables in the discriminant analyses, the number of variables was further reduced by retaining only those which improved classification accuracy, as indicated by a pseudojackknife test (see BMDP documentation; Lachenbruch and Mickey 1968).

Best results were obtained with the following input variables: MW and MWI, SPL or AGL, API or AGI, TLI or NGI, and ASP or AEOV (Tables 1, 2). In males 94.6% correct classification (Table 2) was obtained using only the three most important variables, SPI, MWI, and TLI (determined by their order of entry into the stepwise analysis), while 96.6% of the females were correctly classified using the first four variables—AEO, AGI, MWI, and NGI. Stage 2 squid were incorrectly classified 19% in males and 10.7% in females, but other squid were correctly grouped in at least 90% of the cases. A plot of the

TABLE 2.—Classification of *Loligo pealei* into stages of sexual maturity using linear discriminant functions. The variables to be measured are listed below with their coefficients or weighting factors for each maturity stage. To classify an individual, construct four linear equations, one for each stage, using the measured values and the appropriate coefficients and constant and solve. The equation resulting in the largest value indicates the stage into which the individual has been assigned.

	Stage			
	1	2	3	4
Variable:				
Males:				
SPI	−949.083	−838.030	−972.007	596.250
MWI	112.680	88.635	92.161	16.472
TLI	7.445	65.620	133.984	130.547
Constant	−49.822	−39.961	−60.416	−35.921
			94.6% correctly classified	
Females:				
AEO	9.695	9.440	13.297	28.915
AGI	−71.476	82.104	233.148	282.733
MWI	98.606	83.025	67.263	76.922
NGI	−26.426	−10.377	54.122	35.443
Constant	−46.310	−37.240	−49.256	−105.526
			96.6% correctly classified	

Example: Assume squid is male.
Then,
$Y(1) = -949.083 \times SPI + 112.680 \times MWI + 7.445 \times TLI - 49.822$

$Y(4) = 596.250 \times SPI + 16.472 \times MWI + 130.547 \times TLI - 35.921$,
where SPI, MWI, TLI are the actual values for the squid in question.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

mean values of the first and second canonical variates for each stage (Anderson 1958) (Fig. 2) shows that stages 1-4 follow a logical sequence from immaturity to ripeness. The first two canonical variates are the orthogonal pair of linear combinations of the variables which best discriminates between the groups. Mean values for the final discriminant function variables are listed in Table 3. Typical DML's for each of the sex-stage groups have also been included for reference.

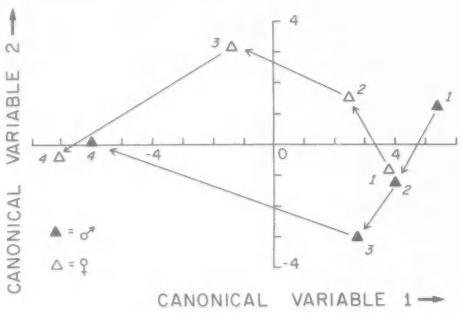


FIGURE 2.—Canonical variates for each stage of sexual maturity evaluated at the stage or group means for each sex. Trajectories between subsequent stages are indicated by arrows.

The Classification Process

To determine the stage of maturation of a squid, the sex must first be determined. If this cannot be done by visual inspection, the squid is considered juvenile (stage 0). Otherwise, DML and MW, plus TL and SPL for males, or NGL, AGL, and EOV for females, should then be determined. From these four or five parameters the appropriate indices needed (Table 2) can be calculated. As indicated in Table 2, a set of four linear equations is then constructed by combining the measured parameter values with the appropriate discriminant function coefficients (weighting factors) and constant listed for each stage. The equation with the largest solution indicates the stage into which the squid should be placed. Thus, once the raw data have been measured and recorded, the actual classification can be done at a later date using even a simple hand calculator. If the raw data are stored on a computer-readable medium, as was done in this study, the process is particularly efficient.

To investigate the broader applicability of the classification, additional squid from the 1976 Narragansett Bay and *Cryos* samples were classified. The discriminant analysis was then performed on these new data to see if the same four stages were identifiable. Over 98% of the individ-

TABLE 3.—Typical mean values (1 SD) of selected maturity stage variables of *Loligo pealei*, listed by sex and stage of development. With the exception of mantle length values (DML), which are from a much larger pooled sample from 1976 to 1978, the reproductive character means are those of the 1976 Narragansett Bay and *Cryos* samples used to compute the final discriminant functions listed in Table 2. Variable coding follows that of Table 1.

	Stage			
	1	2	3	4
Variable:				
Males:				
TLI (%)	11.6 (3.62)	19.0 (3.70)	30.7 (3.73)	30.3 (4.45)
MWI (%)	85.8 (6.90)	71.7 (7.51)	78.0 (8.74)	53.2 (11.71)
SPI (%)	0	0	0	3.6 (0.93)
n	131	119	42	383
DML (cm)	7.1 (2.17)	11.1 (3.25)	10.8 (4.67)	18.6 (8.03)
n	506	610	159	708
Females:				
AEO	1.0	1.0	1.8	4.7
AGI (%)	0	2.6 (1.00)	5.2 (2.62)	5.7 (1.27)
MWI (%)	83.6 (7.98)	74.7 (8.09)	65.0 (11.12)	61.4 (9.25)
NGI (%)	7.8 (3.23)	11.4 (4.86)	24.0 (3.74)	25.8 (4.24)
n	243	124	64	262
DML (cm)	7.8 (2.24)	11.4 (3.09)	13.6 (4.47)	14.3 (3.99)
n	947	467	155	498
Juveniles:				
MWI (%)	97.3 (10.24)			
n	1,857			
DML (cm)	4.6 (1.13)			
n	1,887			

uals of both sexes were correctly grouped, and the new discriminant functions did not differ appreciably from the original ones. Thus the method was shown to be internally consistent (precise). Accordingly, during 1977 and 1978 only the four or five measurements necessary for classification purposes were routinely taken.

The Four Maturity Stages

A description of the general characteristics of each of the four maturity stages of *L. pealei* follows. Figures 3a and b illustrate the important morphometric changes indicated by the discriminant analysis results.

Stage 0: These juvenile squid lack visible gonads (Fig. 3a) and are very broad for their length.

Stage 1: In females (Fig. 3a) the nidamental glands appear as thin white streaks, averaging 8% of DML (Table 3). In males the testis appears as a pale oval body, about 11% of DML, and is frequently obscured by the stomach and caecum.

Stage 2: Both the nidamental glands and testis have almost doubled in length, to 11% and 19% DML, respectively, and the accessory and oviducal glands of females or the spermatophoric organ/Needham's sac complex of males becomes evident. The ovary appears as a fine-grained band of tissue.

Stage 3: This is a transitional stage between immaturity and maturity. The NGI and AGI have approximately doubled again (24% and 5% DML), and the translucent white immature ova give the ovary a distinctly granular appearance (AEO = 2 or 3). The TLI averages 31% DML (Fig. 3b; Table 3), and immature spermatophores may be visible as small white specks in Needham's sac (ASN = 2). No gametes can be found in the penis or oviduct, however.

Stage 4: In these mature squid (Fig. 3b), much of the mantle cavity is occupied by the bulging ovary and oviduct or by the testis. Ripe eggs fill the oviduct and appear as amber spheres 1-2 mm in diameter (AEO>3, AEOV>1). Elongate mature spermatophores (ca. 5 mm long) are visible both in Needham's sac and in the penis (ASN, ASP>1). Immature ova are also found beneath the ripe eggs in the ovary, and usually the spermatophore receptacle is packed with spermatophores. A few virgin females were seen, however.

An Application of the Method

Insights into the usefulness and relevance of the new classification system can be provided by a brief examination of several findings of the overall population study of which this was a part (Macy 1980). Vovk (1972) distinguished between ripe/mature squid and spent squid, but throughout 1975 when the Vovk method was routinely employed, no spent squid were positively identified. Subsequent statistical analysis also failed to make this distinction. Laboratory observations (Macy 1980), however, suggest a reasonable explanation: Isolated females spawned repeatedly over 2-3 wk, but still contained significant numbers of immature eggs; neither sex ceased feeding after mating; and no evidence of nutrient depletion was found. Thus no truly spent individuals might be expected.

Maturing squid, on the other hand, were abundant in late winter prior to the onset of inshore migrations. In the March 1978 *Argus* samples, stage-3 squid constituted 35-40% of the population, while only 8% of the females and 21% of the males had yet reached maturity (stage 4). About 1 mo later (late April) large mature squid began to arrive and spawn in Narragansett Bay. By late July most spawning activity was completed, but already stage-1 individuals from early spawnings were becoming numerically dominant. By the time of arrival offshore, in late fall and early winter (*Cryos* and *Argus* 1977 samples), fewer than 6% of either sex were mature or maturing, but over 50% of the population was composed of stage-2 squid.

These early winter stage-2 squid seem to represent two distinct age/maturity groups: Smaller developing young of the year, and larger and presumably older squid whose gonads appear to be resorbing or regressing. The 1976 *Cryos* sample, for example, consisted of three groups of males with modal lengths of 8.2, 11.6, and 19.1 cm. Only 4.5% of these males ($n = 287$) were mature (stages 3, 4), but 71.4% were at stage 2. The modal size of the stage-2 squid lay between 10 and 12 cm, but individuals ranged from 8 to 23 cm. The remaining stage-1 squid had a modal length of only 8-9 cm. Regressing stage-2 individuals belonged to both the 11.6 and 19.1 cm size classes. Their gonads had the coloration and approximate length of more mature individuals, but were distinctly thin and lacked eggs or spermatophores of any size.

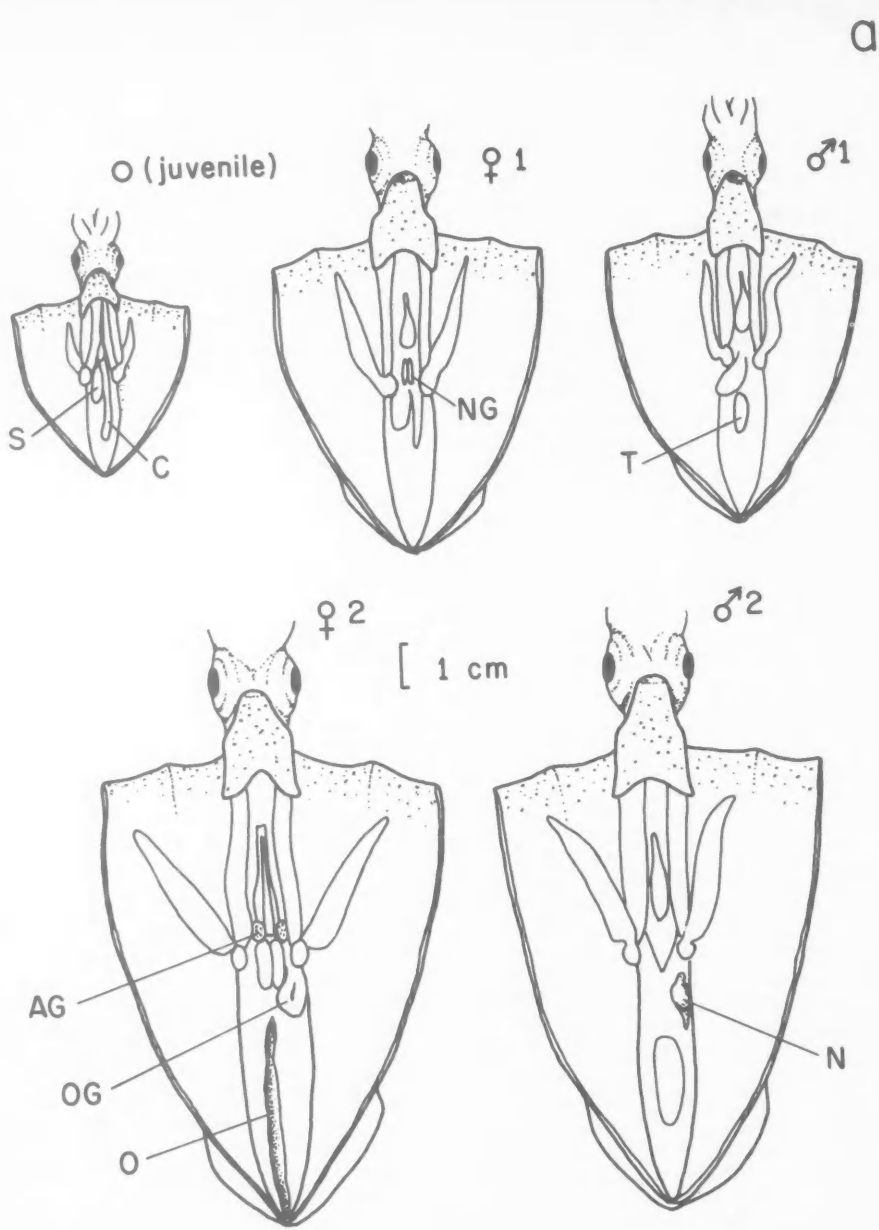
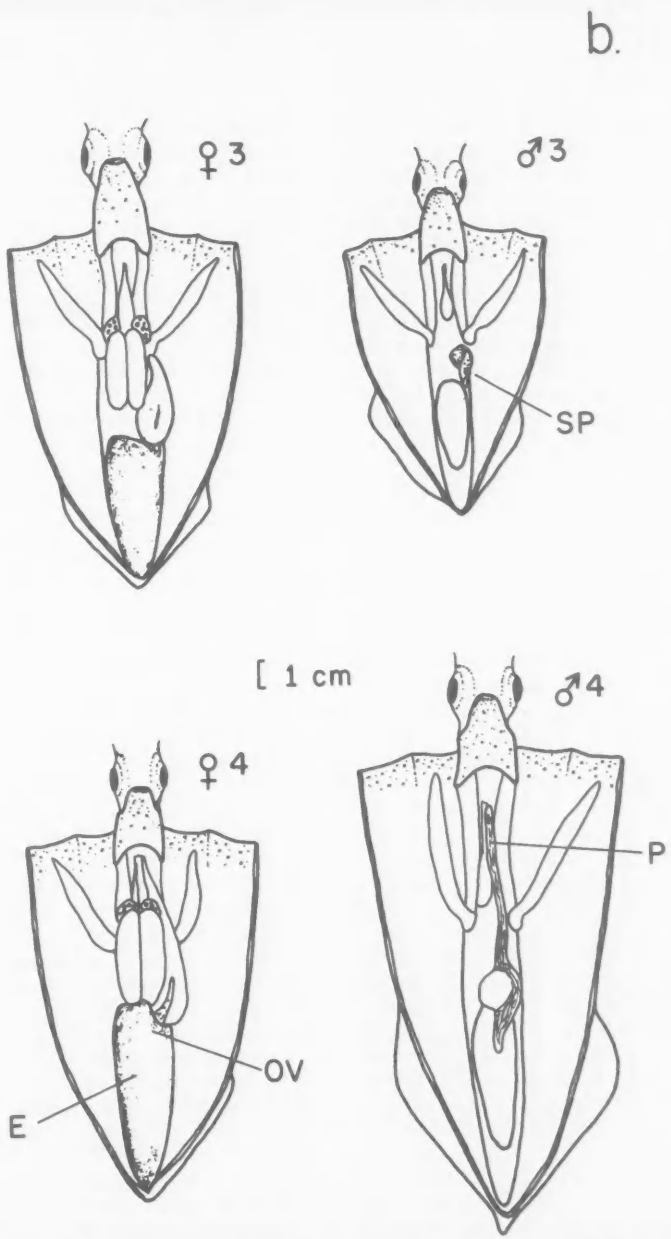


FIGURE 3.—Squid of each stage of maturity illustrating those morphometric changes which the discriminant analysis showed to be important. a, Juvenile and immature squid (stages 1, 2). b, Maturing and mature or ripe squid (stages 3, 4). The diagrams are drawn to scale using the mean values of the morphometric characters given in Table 3 for each sex-stage



combination. S = stomach; C = caecum; NG = nidamental glands; T = testis; AG = accessory glands; OG = oviducal gland; O = ovary; N = Needham's sac/spermatophoric organ complex; SP = spermatophores; E = egg mass (mature); OV = oviduct; P = penis. Digestive tracts are not shown in stages 3 and 4 (Fig. 3b).

DISCUSSION

A classification system should have two major attributes: It should be objective and easy to employ, and it should be biologically meaningful. The major impediment to satisfying both concerns appears to be the high degree of variability which exists within and between populations of *L. pealei*. This species has a wide geographic range, from the coast of South America to Nova Scotia (Cohen 1976), and thus populations living in different parts of the range are exposed to different and varying environmental conditions (temperature, salinity, photoperiod, and food availability) throughout their respective annual cycles. Such environmental variation is manifested by both spatially and temporally varying growth rates, which result in the presence of multiple cohorts within a year class (Summers 1968, 1971; Mesnil 1977; Lange and Johnson 1979), and by differences in the timing of inshore movement and gonad maturation (Hixon 1980; Macy 1980). Thus it is evident that samples used to construct a sexual development classification should at least reflect both the inshore and offshore portions of the range. This was done (Fig. 1). The Vovk (1972) classification, however, was based only on offshore collections, and as a result probably included relatively few spawning individuals and young of the year in early development. Summers (1968, 1969, 1971), on the other hand, sampled both inshore and offshore, but distinguished only between mature and immature individuals.

Objectivity and Utility of the Multivariate Approach

The multivariate approach to the classification problem is appropriate and objective when geographic (environmental) variability of unknown magnitude is superimposed on the usual random variation among individuals, producing the observed age or size and reproductive structure of the population or species. This is true because the analytical approach used here can effectively integrate the information and provide a simple numeric classification rule. Growth rates for *L. pealei* have only been estimated from modal size progressions (Summers 1971; Mesnil 1977), and hence the age of an individual or cohort can only be roughly estimated. Since multiple cohorts occur even within a small area (Narragansett Bay), mean and standard deviation values of morphometric characters, such as of DML or GW, have limited value for discrimination because of the large variability range of individuals (i.e., multimodality). It is known, for example, that considerable variation exists in the age or size of *L. pealei* at spawning (Haefner 1964; Summers 1971; Macy 1980). Standardization by the use of ratio parameters or indices may provide a partial solution to the variability problem.

In the interest of speed and ease of measurement, a set of nominal variables to assess the relative abundance of eggs or spermatophores (ASN, ASP, AEO, AEOV; Table 1) was used in addition to the ratio or interval variables (MWI, TLI, SPI, NGI). The "none," "some," "many" rating scale is not strictly objective, but such coarse evaluations can be done reliably with little training and have proved to be valuable discriminators. Theoretically it is possible to develop an entirely objective classification system. In practice, a somewhat more subjective approach usually proves necessary. What other investigators have found important in distinguishing different maturity groups, such as gonad to body weight ratios (Hayashi 1970), must certainly influence the initial selection of variables to be measured. The investigator must also decide how detailed a classification is desired and what additional parameters may be required. Repeated use of the exploratory technique of cluster analysis followed by stepwise discriminant analysis, as employed here, provides a way of learning how many groups may be present and how to "best" identify them using only those variables which can be shown to significantly aid discrimination. But, at this stage too, the researcher must at least roughly determine the basis for case clustering (by size, color, sexual development, etc.).

Biological Relevance and Accuracy

Statistically accurate and precise results may prove meaningless in reality. Thus the most important verification of the classification scheme is the demonstration of biological relevance in the appropriate context. In each of the 2 yr when the system was routinely employed, a predictable and logical progression of sexual development from hatching to spawning was observed. Moreover, the findings which resulted from this application of the method are reasonable and have significant, broader implications.

Laboratory studies confirm evidence from the field that spent squid cannot be reliably distinguished from spawning squid, even though the majority of samples (Narragansett Bay) were taken on the spawning grounds during the peak of reproductive activity. Hixon (1980) was also unable to find spent *L. pealei* or arrow squid, *L. plei*, in the Gulf of Mexico, and he too documented multiple spawning by *L. pealei*. Furthermore, it has been shown histologically (Burukovski and Vovk 1974) that egg development is highly asynchronous among individuals, and that a series of eggs at different stages of development in the ovary is typical. Prolonged spawning by poorly synchronized individuals of a population would tend to extend spawning over time, and may well account for the lack of reports of dead or dying squid of this species on the spawning grounds.

Stage-3 individuals, particularly males, were poorly sampled during 1976 (Table 3). This was expected since only fully mature individuals move inshore in large numbers, and reproductive development ceases or regresses in late fall. These animals show the first obvious signs of approaching maturity: Developing eggs and spermatophores may be visible, and the nidamental and accessory glands of females and the testes of males (Table 3) have reached sizes comparable to those of fully mature squid. The stage may be of short duration, since gonad development appears to be rapid offshore, with large squid, especially males, maturing faster than the smaller ones (Summers 1969; Macy 1980). In the March 1978 *Argus* samples, large numbers of stage-3 squid were identified, and it is unfortunate that other late winter or early spring offshore samples were not available to better document the latter stages of maturation.

The relatively low classification accuracy of the method for stage-2 squid (81% for males) probably is due to the wide size range of these individuals in the fall and early winter, and to the unusual gonad development of the larger individuals. Sexual regression by gonad resorption to a neutral or inactive state, though relatively common in bivalve molluscs (Sastry 1979), appears to be rare in cephalopods. Regression has been suspected in *L. pealei* (Summers 1971; Vovk 1972; Arnold and Williams-Arnold 1977) and possibly also in European common squid, *L. vulgaris* (Tinbergen and Verwey 1945), however. The phenomenon could explain why only a few of even the largest squid (20 cm and larger DML), thought to be in their second year (Summers 1971; Mesnil 1977), are mature in the late fall and early winter offshore samples. Lacking a reliable means of aging this species, it is not currently possible to prove that the larger "regressed" squid are in fact older than their smaller developing stage-2 counterparts. It is also possible that sexual maturation merely halts at the onset of winter and resumes again in January or February prior to onshore migrations. This hypothesis does not explain why the gonads appear to be shrinking, nor would it account for the presence of both very large and small squid at the same stage of development. Unfortunately, *L. pealei* has not been held sufficiently long in captivity to confirm either supposition.

Comparisons with Other Classification Methods

The main assets of the classification method presented here are its objectivity and its ease and speed of use. To be sure, the development took considerable time, especially interpretation of early cluster analyses, but the basic strategy is relatively straightforward and does have internal accuracy checks. If a more detailed breakdown of the maturation process were desired, e.g., to examine details of gametogenesis, the same analysis techniques could be applied to objectively identify and separate the various phases. Thus the methodology should be applicable to a wide range of biological problems.

When compared with several other classification systems, the advantages of the present method become more evident. Two basic classes of systems exist. Those used by Tinbergen and Verwey (1945), Holme (1974), Juanicó (1979), and Hixon (1980) are mainly qualitative, in that the presence or absence of one or more characters, considerations of color or texture, and estimation of relative sizes or gamete abundance are used. The other group of classification schemes, typified by those of Mangold-Wirz (1963), Hayashi (1970), Vovk (1972), and Durward et al. (1978) are quantitative methods. These schemes may employ one or more subjective judgments or estimates, but rely mainly on objective characters such as relative organ lengths or weights, egg diameters, or spermatophore lengths (absolute or relative) to distinguish successive maturity stages. Both types of classification systems are of value, but only the latter group will be discussed further because their methods are more objective and

perhaps more suitable for large-scale applications.

There are obvious similarities between this classification and that of Vovk (1972), and it appears that, except for stage-5 spent squid, the maturity stages are comparable in both systems. It should be reiterated, however, that the stage characteristics and average parameter values given in this report (Fig. 3a, b; Table 3) were identified after the classification functions had been determined, whereas in the Vovk system the stage indicators form the basis for classification. The offshore squid sampled by Vovk also appear to have been larger by at least 3-5 cm at each stage than those used in this study. Thus, NGL indices in the Vovk study are 6.4-25% greater than those given in Table 3. A TLI, surprisingly, was not used. Vovk did employ hectocotylus length, but in *L. pealei* the hectocotylized arm may be difficult to identify, particularly in small males, and, more important, may be lost or damaged during trawl capture of squid. These and other smaller differences between the methods appear to result mainly because Vovk did not sample the actively spawning inshore population. His method generally works well for experienced personnel, but dissection and weighing of the reproductive tracts and weighing the whole squid take more time and equipment than may be available in the field. At least two more characters must be recorded for each sex as well.

Two simple but objective classifications were developed for Japanese squid, *Todarodes pacificus* (Hayashi 1970) and for female short-finned squid, *Illex illecebrosus* (Durward et al. 1978). Hayashi computed a numerical index, M, equal to the weight of Needham's sac (NW) divided by NW plus the testis weight, or to the oviduct weight (odW) divided by odW plus the ovary weight. If the computed value of M is <0.5, equal to 0.5, or between 0.5 and 1.0, the squid is considered immature, mature, or spent, respectively. Since spent *L. pealei* are at least rare, the system reduces to a two-stage classification which offers no obvious advantage over the immature-mature distinction used by Summers (1968). The dissection and weighing of the two tissues are additional drawbacks.

Durward et al. (1979) used data initially obtained from six *I. illecebrosus* which matured in captivity but had not spawned to develop a five-stage maturity scale for females. These investigators showed (by scatter plots and regression analyses) that relative NGI's correlated well with identifiable stages of ovarian development. Thus only two parameters, DML and NGL, were needed for classification. As Durward et al. have pointed out, the critical values of the NGI for *Illex* for the first four stages are very similar to those for *Loligo* (Table 3). However, in *L. pealei* NGI ranked last of four variables in importance (Table 2), and even the most significant variable (AEO) alone yielded only 77.8% correct classification accuracy. This simple and objective classification for *Illex* is now widely used (Amaratunga and Durward 1979).

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BIOENERGETICS AND GROWTH OF STRIPED BASS, *MORONE SAXATILIS*, EMBRYOS AND LARVAE

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ABSTRACT

Fluctuations in year class size of striped bass are known to be related to development and survival in the early life stages. Bioenergetic aspects of growth and development of striped bass embryos and larvae were determined in the laboratory to discover some of the physiological needs and processes of these stages from fertilization to metamorphosis.

Energy was provided by endogenous (yolk and oil globule) and exogenous (*Artemia* sp.) sources. Initial amounts of yolk and oil varied significantly among eggs from seven different females, and these differences were reflected in different patterns of consumption and growth. Feeding larvae consumed their endogenous oil at rates related to exogenous food intake. Daily food rations of larvae from the onset of feeding to metamorphosis were estimated for field and laboratory conditions. Rations increased with size and age of the larvae. Wild larvae were estimated to have daily rations substantially greater than those of cultured larvae.

Energy outputs were measured in growth and oxygen consumption. Egg size (total dry weight) directly influenced early periods of growth, but later compensatory growth, seen in more rapid growth in larvae from smaller eggs, made up for initial differences. Growth and food consumption were linearly related and, again, different growth characteristics were seen in each batch of fish. Embryos and prefeeding larvae had the highest Q_{O_2}, while metabolism on a weight-specific basis increased with tissue dry weight and was best described by a power function.

Gross caloric conversion efficiencies were highest from fertilization to initial feeding. Feeding larvae used their resources at levels under 20% and their conversion efficiencies did not appear to correlate with food concentration.

In an energy budget model, striped bass embryos and larvae given the highest food density consumed yolk energy at constant rates until totally absorbed. Oil globule consumption fluctuated in relation to growth and nonassimilation, rising sharply after first feeding then declining as food intake increased. Metabolism fluctuated according to developmental stage, rising with the onset of active feeding. Nonassimilation steadily increased as larvae relied more on exogenous food.

Striped bass, *Morone saxatilis*, populations have fluctuated historically throughout their ranges, but in recent years they have declined consistently and unexplainably, especially on the west coast of the United States. Present estimates place the population of the San Francisco Bay/Delta estuary at 33% to 40% of its 1960 peak abundance and it is forecasted to decline further (Stevens 1980). Despite availability of considerable information on striped bass (Pfuderer et al. 1975; Rogers and Westin 1975; Horseman and Kernehan 1976; Setzler et al. 1980), factors that control or influence these fluctuations and declines are not known. Field researchers concluded from 20 yr of data collection that year class size directly correlates with survival and growth during the first 60 d of life and this, in turn, is controlled by environmental conditions—principally the interrelated factors of freshwater flow, water diversion, and food supply (Stevens 1977a, b; Chadwick 1979[2]; Stevens 1980).

To determine the direct causal mechanisms operating between these environmental conditions and early life stage growth and survival, we conducted a series of laboratory experiments over a 6-yr period. Our working hypothesis was that a combination of inherent and environmental factors determined the ability of striped bass embryos and larvae to meet metabolic requirements for successful growth and survival to the pivotal age of 60 d. These factors involve a variety of physiological, morphological, and behavioral functions, and are controlled and/or limited by environmental conditions. Whole organism

[1]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

[2]Chadwick, H. K. 1979. Striped bass in California. Prepared for U.S. Environmental Protection Agency, Region II, 27 p.

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FISHERY BULLETIN: VOL. 80, NO. 3, 1982.

bioenergetics was selected as our approach because it represents these functions in an integrated and comprehensive fashion.

Bioenergetics of adult fishes has been studied for some time (Ivlev 1939a, b; Winberg 1956; Warren and Davis 1967; Brett and Groves 1979). As interest in fish eggs and larvae grew, knowledge gained from studies of adults was applied toward research on early life stage energetics (Toetz 1966; Laurence 1969, 1971, 1977; Cooney 1973). Most of these publications are concerned with the critical period when larvae begin active feeding and change from endogenous to exogenous energy sources (May 1974b). Other researchers have used bioenergetic studies to assess the effects of pollutants or other environmental conditions on larvae (Laurence 1973; Eldridge et al. 1977).

Our early research on striped bass embryos and larvae has already been reported (Eldridge et al. 1981). Emphasis was on factors associated with food and feeding of larvae and how they related to mortality, point of no return, development, and, to a limited extent, energetics. The research presented here is a detailed analysis of the energy sources, endogenous and exogenous, and their influence on energy outputs in the early life stages of striped bass.

MATERIALS AND METHODS

Energy Input Determinations

Component analyses of eggs prior to fertilization were done on eggs from seven different females used for embryo and larval studies and on 34 ripe fish collected at random from natural spawning areas. All eggs came from fish from the Sacramento River, Calif. Three replicates of 25 eggs each were weighed fresh after brief blotting on absorbent filter paper, then dried to constant weights at 60°C and reweighed to yield water contents and total dry weights. Yolks and chorions were dissected from Formalin[3]-preserved eggs with microdissection tools; they then were dried and weighed to the nearest 0.1 μg. These amounts were then subtracted from the total weight to provide oil weights. Total lipid contents were obtained by 2:1 chloroform-methanol extraction in micro-Sohxlet apparatus. Our procedure for caloric determinations of yolk and oil involved whole egg homogenization followed by centrifugation to separate yolk, oil, and chorion membrane components. Yolk and oil were then aspirated into dishes, oven dried to constant weights at 60°C, and bombed according to standard microbomb calorimetric methods. Estimates of tissue and *Artemia* caloric contents were made from homogenates of whole animals, the larvae being sampled after complete oil globule consumption. All caloric contents are expressed as calories per gram ash-free dry weight.

All measurements of yolk and oil volume and lengths were done with ocular micrometers in dissecting microscopes. All measurements and determinations were performed at least in duplicate and, if possible, in triplicate.

Eggs from seven different females were fertilized artificially according to methods of Bonn et al. (1976). Eggs were incubated in McDonald jars. After hatching, larvae were transferred to hemispherical 8 l acrylic plastic containers held in water tables to stabilize temperature. Initial stocking densities were approximately 150 larvae/container. In three of the seven batches, larvae were reared to the age when feeding begins, 7 d after fertilization (D-7). The remaining four batches were reared to 29 d after fertilization (D-29). During the process we attempted to duplicate natural water quality conditions as much as possible. Temperatures were maintained at 18°C, and oxygen content was at or near saturation throughout the experiments. Photoperiod and light qualities were kept close to natural. Salinities were zero from fertilization to D-4, 1.0‰ from D-5 to D-13, and 3‰ from D-14 to D-29. Each day containers were cleaned and new water and food were added. An endemic small (1-2 μm) green phytoplankter (*Nephroselmus* sp.) was also added in concentrations of 10^2-10^3/ml.

Larvae began feeding consistently on D-7, at which time they were given newly hatched, live *Artemia salina* nauplii (San Francisco Bay Brand). The range of initial food concentrations was selected to include the estimated natural zooplankton densities (0.003 to 0.010/ml (Daniel 1976)) and the concentrations used in other striped bass research. Initial concentrations were 0.00, 0.01, 0.10, 0.50, 1.00, and 5.00 *Artemia*/ml.

To estimate daily exogenous food rations of larvae we used the following formula: daily food ration = (average stomach contents)(hours of active feeding)/digestive time. Detailed studies

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

on diel feeding patterns and evacuation rates of larvae in our experimental systems were conducted in the early stages of this study and were presented in Eldridge et al. (1981). Because larvae in all food concentrations consumed their food within 10 h after food was first introduced, we selected 10 h/d for use in the above formula. We found that sampling larval stomachs 1 h after food introduction was most representative of average stomach contents during the active feeding periods. A minimum of 10 larvae was dissected and the stomach contents were quantified for each food ration estimate for each experiment. Evacuation rates of food ingested by larvae which were feeding continuously ranged from 1.5 to 5.5 h with an overall average of 3.3 h. Times of 100% evacuation were combined for different-aged larvae and used in this study (Table 1).

TABLE 1.—Average times (h) required for *Artemia* nauplii to pass through the digestive tracts of continuously feeding striped bass larvae.

Age (days after fertilization)	Food concentration (*Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9-16	3.3	4.0	3.5	4.5	4.0
17-24	2.5	2.8	3.5	3.5	2.3
25-29	2.5	2.5	3.7	4.0	3.0

Energy Output Determinations

Growth of embryos and larvae was measured by carefully removing all yolk and oil globules from Formalin-preserved specimens, rinsing the remaining tissues in distilled water, drying at 60°C, and weighing to the nearest 0.1 μg. Measurements were in duplicate with 3 to 5 specimens per sample. Standard lengths of larvae were measured to the nearest 0.1 mm with an ocular micrometer. Duplicate measurements of 20 larvae each were done. Preserved specimens were measured as soon as possible. The entire set of samples from each experiment required an average of 8 wk to process.

Oxygen consumption was used as a measure of "routine" metabolism (Fry 1971) and was measured with standard manometric techniques using a differential microrespirometer. At least five replicate samples (from 5 to 50 animals/sample depending on age and size) were taken at each test period. Sampling occurred at D-0.5, -1.0, -2.0, -4.0, and on each even day until D-30 (time measured from time of fertilization).

RESULTS

Energy Inputs

Endogenous Sources

Initial sources of energy for striped bass embryos and early larvae are yolk and oil, the latter contained in a single large globule. The relative composition of these egg components was found to vary considerably between the seven different females used in rearing experiments (Table 2). Oil accounts for most of the variability in dry weight, whereas yolk is more variable in measurements of volume. Caloric contents of these two energy sources were consistent, which indicates that variability of total energy in the egg results from differences in absolute amounts of oil, yolk, or both, rather than differences in the energy content of those materials. Eggs from different females contained widely ranging

TABLE 2.—Dry weights, volumes, and caloric contents of striped bass eggs and egg components at time of fertilization. Three replicates of 25 eggs each were used for dry weights, three replicates of 20 eggs each for volumes, and two replicates of approximately 50 mg (dry weight) were used for caloric content determinations.

Experiment no.	Mean dry weight (mg)				Mean volume (mm^3)		Caloric content				
							yolk		oil		total
	yolk	oil	chorion	total	yolk	oil	cal/g	cal/egg	cal/g	cal/egg	cal/egg
1	0.114	0.150	0.022	0.286	0.67	0.21	5,687	0.648	9,223	1.383	2.031
2	0.089	0.137	0.023	0.249	0.65	0.20	5,720	0.509	9,360	1.282	1.791
3	0.131	0.089	0.028	0.248	0.57	0.13	5,622	0.736	9,133	0.813	1.549
4	0.106	0.251	0.016	0.373	0.52	0.21	5,641	0.596	9,869	2.477	3.073
5	0.118	0.189	0.014	0.321	0.20	0.17	5,635	0.665	9,627	1.819	2.484
6	0.089	0.128	0.014	0.231	0.38	0.18	5,635	0.502	9,738	1.247	1.749
7	0.083	0.115	0.012	0.210	0.62	0.14	5,625	0.467	9,655	1.110	1.577
$\bar{x}$	0.104	0.151	0.018	0.274	0.516	0.177	5,652	0.589	9,515	1.447	2.036
SE	0.018	0.054	0.006	0.057	0.170	0.033	37	0.100	278	0.546	0.558
Range	0.089– 0.131	0.089– 0.251	0.012– 0.028	0.210– 0.373	0.20– 0.67	0.13– 0.21	5,641– 5,720	0.467– 0.736	9,133– 9,869	0.813– 2.477	1.549– 3.037
C.V.	17.3	35.6	33.0	20.8	33.0	18.4	0.7	16.9	2.9	37.7	27.4

amounts of yolk and oil (coefficients of variation 27% and 25% for yolk and oil, respectively) and little (<3%) difference was found in energy contents. The oil globule accounted for an average 55% of the dry weight and 71% of the total energy of the egg. Yolk accounted for 38% of dry weight and 29% of energy. The two sources combined provided an average 2.036 cal/egg.

Yolk contained an average 5,652 cal/g, which agrees with Phillips' (1969) estimate of 5,660 cal/g gross energy for digested protein. Lipid extraction analyses of yolk from three of the seven spawned females showed that only 3.8% of dry weight was lipid material.

Embryos and larvae from the seven different females consumed their yolks linearly (Fig. 1). At hatching an average 58% of the original yolk energies remained, and they were totally utilized between D-6 and D-7, the time when active feeding began. Analyses showed no significant differences in yolk utilization rates but highly significant differences in intercepts ($P \leq 0.01$), further indication of the differences in original yolk reserves.

Initial oil energy contents per egg ranged from 0.8 to 2.5 cal (Table 2) and differed significantly between batches ($P \leq 0.05$). An average 86% of these initial amounts remained at hatching and 71% was present on D-7. Analyses of covariance indicated that the utilization rates from fertilization to feeding (Fig. 2) also were significantly different ($P \leq 0.05$). With the exception of one batch, embryos and larvae consumed their oil energies so that approximately the same amounts of energy remained on D-7.

The rates at which oil globule calories were utilized and the ages at complete oil energy absorption (D-20 to D-29) appeared related to food concentration (Fig. 3). Starved larvae and those in 0.01 *Artemia*/ml concentrations conserved oil, whereas those fed progressively higher concentrations consumed energy at faster rates. Analyses of covariance showed significant differences in oil consumption among batches within each food concentration. Tests of food concentrations and oil consumption within batches showed all to have highly significant differences ($P \leq 0.01$) in intercepts, and two of the four batches had significant slope differences ($P \leq 0.05$).

Exogenous Sources

Larvae in all experiments began active feeding 5 d after hatching. Average stomach contents, presented as the average number of ingested *Artemia* and their equivalent calories, are presented in Table 3. These data were further used to calculate daily food rations (Table 4). With some exceptions, larvae increased their exogenous energy intake in direct relation to food availability and age in all food concentrations except 0.01 *Artemia*/ml. Larvae in this low concentration showed no particular trend.

Energy Outputs

Growth

Embryonic and prefeeding larval growth, measured in assimilated tissue calories, differed significantly among the seven batches ($P \leq 0.01$).

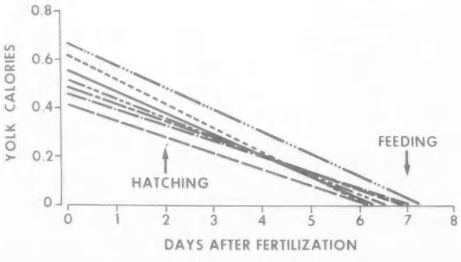

FIGURE 1.—The consumption of yolk calories by seven different batches of striped bass embryos and larvae cultured under identical conditions.

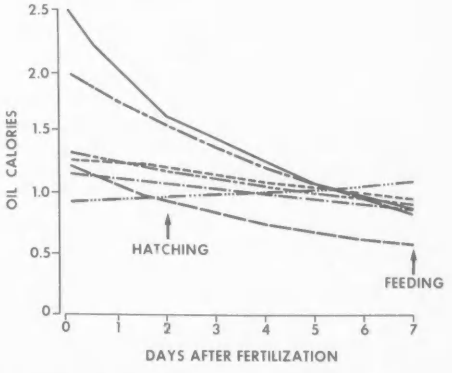

FIGURE 2.—The consumption of oil globule calories by seven different batches of striped bass embryos and prefeeding larvae.

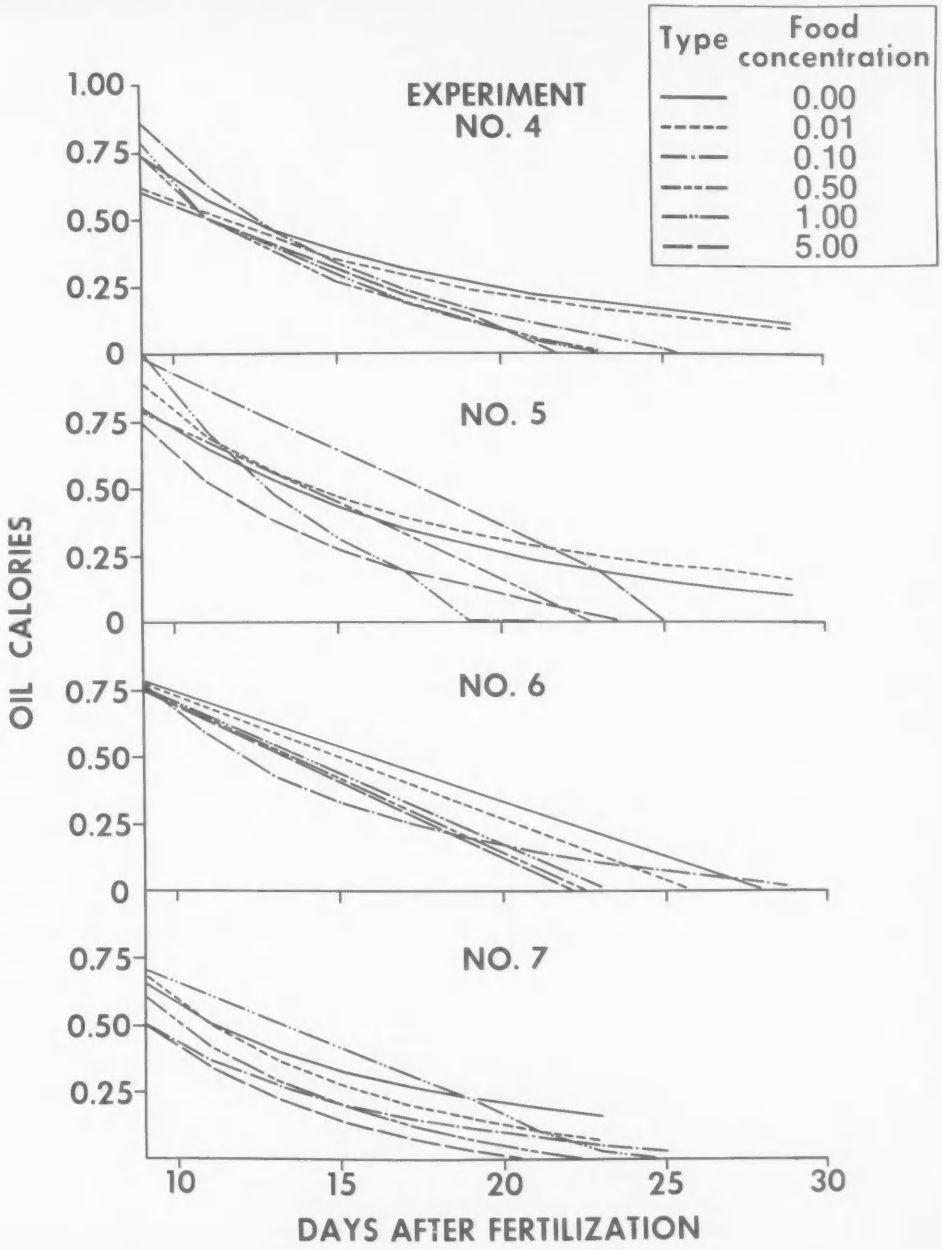

FIGURE 3.—The consumption of oil globule calories by striped bass larvae from four different batches (experiments 4-7) fed six different food concentrations (0.00 to 5.00 *Artemia*/ml).

TABLE 3.—Average stomach contents and their corresponding caloric equivalents of striped bass larvae feeding at different food concentrations from 9 to 29 d after fertilization. Presented as number of food organisms/number of calories per larva.

Age (days after fertilization)	Food concentrations (no. *Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9	0.05/0.001	0.15/0.001	5.40/0.052	4.30/0.041	7.60/0.073
11	0/0	0.85/0.008	7.50/0.072	11.70/0.112	2.80/0.027
13	1.50/0.014	3.30/0.032	9.20/0.088	18.40/0.177	9.890/0.094
15	0.05/0.001	4.10/0.039	23.10/0.222	24.00/0.231	10.20/0.098
17	0.15/0.001	8.40/0.081	27.10/0.260	39.40/0.39	18.60/0.179
19	0/0	12.50/0.120	29.50/0.283	33.30/0.320	24.60/0.236
21	0.15/0.001	13.00/0.125	26.10/0.251	40.00/0.384	33.70/0.324
23	4.16/0.040	14.20/0.136	47.40/0.456	35.90/0.345	53.00/0.509
25	1.10/0.001	57.20/0.550	17.00/0.163	83.10/0.799	59.40/0.571
27	0.25/0.002	470/0.045	65.40/0.628	60.20/0.579	72.40/0.696

TABLE 4.—Estimated daily food ration (number of *Artemia* consumed by one larva in 24 h/equivalent calories consumed in 24 h) of striped bass larvae at different ages feeding at different food densities.

Age (days after fertilization)	Prey densities (*Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9	0.2/0.001	0.4/0.004	15.4/0.148	9.6/0.092	19.0/0.183
11	0/0	2.1/0.020	21.4/0.206	26.0/0.250	7.0/0.067
13	4.6/0.044	8.3/0.079	26.3/0.253	40.9/0.393	24.5/0.235
15	0.2/0.001	10.3/0.099	66.0/0.634	53.3/0.513	25.5/0.245
17	0.6/0.006	30.5/0.294	77.4/0.744	112.6/1.082	82.7/0.794
19	0/0	45.5/0.437	84.3/0.810	95.1/0.914	109.3/1.051
21	0.6/0.006	47.3/0.454	74.6/0.717	114.3/1.098	149.8/1.439
23	16.6/0.160	51.6/0.496	135.4/1.301	102.6/0.986	235.6/2.264
25	1.0/0.010	18.8/0.181	176.8/1.699	150.5/1.446	241.3/2.319
29	11.6/0.111	58.8/0.565	194.3/1.867	288.8/2.775	410.0/3.940

Greater differences were seen in the intercepts than rates, and this, in turn, seemed related to the initial egg sizes (total dry weights). Descriptive equations for assimilated tissue calories of the different experiments are in Table 5. Daily growth coefficients (Laurence 1974) to hatching and to first feeding correlated well with initial egg size. The rate of growth from fertilization to hatching age (avg. $G_W = 1.872$) was three times that to feeding age (avg. $G_W = 0.647$).

Standard lengths at hatching (3.9±0.6 mm), and especially at first feeding (5.8±0.3 mm) (Table 5), also correlated well with initial egg size. Smaller standard deviation of D-7 larvae than of newly hatched larvae (coefficients of variation 5% vs. 15%) suggests larval lengths converged with age.

Growth characteristics of feeding larvae were unique to each batch within each food concentration as was found in earlier stages. Examples are given in Figures 4 and 5 which present growth in tissue calories and standard lengths of larvae fed the high food ration (5.0 *Artemia*/ml).

Within each batch, growth was linearly related to food concentration (Fig. 6). Differences in overall growth are again apparent. Experiment 7 larvae grew fastest.

Larval length-weight relations were exponen-

TABLE 5.—Best descriptive equations (y = tissue calories, x = days after fertilization), initial egg dry weights, standard length, and growth coefficients of striped bass embryos and prefeeding larvae.

Experiment	Initial egg size (μg)	Best fit growth equation (tissue cal)	Standard errors of estimate	Standard lengths (mm)		Daily instantaneous growth coefficients[1]	
				at hatching	at feeding	to hatching	to feeding
1	286	$y = 0.159359\ (x^{0.576582})$	0.0480	4.7	5.5	1.966	0.624
2	249	$y = 0.107496\ (x^{0.847936})$	0.0653	4.0	5.6	1.844	0.630
3	248	$y = 0.133695\ (x^{0.860384})$	0.0446	4.7	5.7	1.733	0.694
4	373	$y = 0.139619\ (x^{0.732174})$	0.0537	3.2	6.1	2.172	0.715
5	321	$y = 0.190165\ (x^{0.767811})$	0.0537	3.2	6.1	2.172	0.715
6	231	$y = 0.090892\ (x^{0.828853})$	0.0187	3.6	5.9	1.763	0.633
7	210	$y = 0.115968\ (x^{0.692895})$	0.0763	3.7	5.4	1.733	0.580

[1]Daily instantaneous growth coefficients = $\log_e W$/days after fertilization where W = dissected tissue dry weight in micrograms.

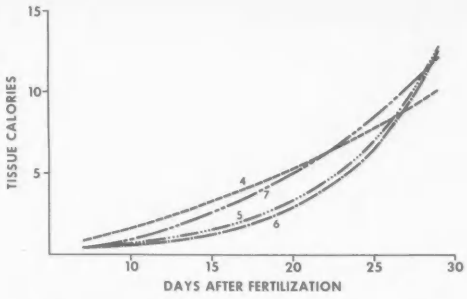

FIGURE 4.—Growth of four batches of feeding striped bass larvae measured in calories of assimilated tissue from first feeding (D-7) to D-29.

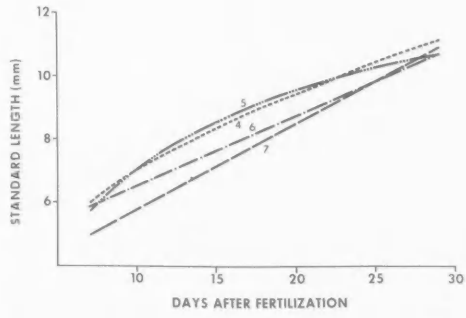

FIGURE 5.—Growth of four batches of feeding striped bass larvae measured in standard lengths from first feeding (D-7) to D-29.

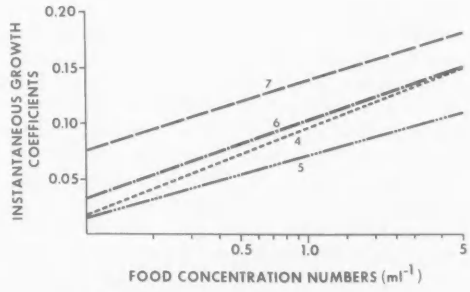

FIGURE 6.—Instantaneous growth coefficients of four batches of feeding striped bass larvae that fed on six different food concentrations (0.00 to 5.00 *Artemia*/ml).

tial for all fish groups (Fig. 7). Experiment 7 larvae were the heaviest per unit length and did not attain the lengths that other larvae did. All larvae put on weight rapidly after reaching a standard length of about 8 mm.

Oxygen Consumption

Metabolic rates of embryos and larvae are presented in Figure 8. Embryos and prefeeding larvae had the highest Q_{O_2}'s. After feeding began oxygen consumption stabilized and remained constant for the duration of the experimental period. On a weight-specific basis oxygen consumption increased with tissue dry weight and was best described by a power function (Fig. 8), although the relationship appears almost linear.

Utilization Efficiency

Gross caloric conversion efficiencies were highest from fertilization to initial feeding, followed closely by efficiencies during the embryonic period (Table 6). Only in larvae from the highest food concentration did conversion efficiencies remain at elevated levels. Larvae feeding at the other food concentrations used their resources at levels under 20%, and their conversion efficiencies did not appear to correlate with food concentration. Starved larvae had the lowest efficiency and demonstrated negligible growth after D-7.

TABLE 6.—Mean gross caloric conversion efficiencies (in percent) for striped bass embryos, prefeeding larvae, and larvae feeding at different prey concentrations.

To hatching	To initial feeding	Food concentrations (*Artemia*/ml) to 29 d after fertilization					
		0.00	0.01	0.10	0.50	1.00	5.00
37.7	43.8	15.0	19.0	13.9	17.3	18.7	31.9

DISCUSSION

Energy Inputs

Striped bass eggs were found to be high in energy content and to vary considerably in size. Undoubtedly the high proportion of lipids (found mostly in the oil globule) makes the striped bass egg one of the most energy-rich of fish eggs. At 7,808 cal/g striped bass eggs exceed the caloric values of eggs from freshwater, anadromous, and marine fishes which normally range from 5,386 to 6,238 cal/g (Hayes 1949; Smith 1957,

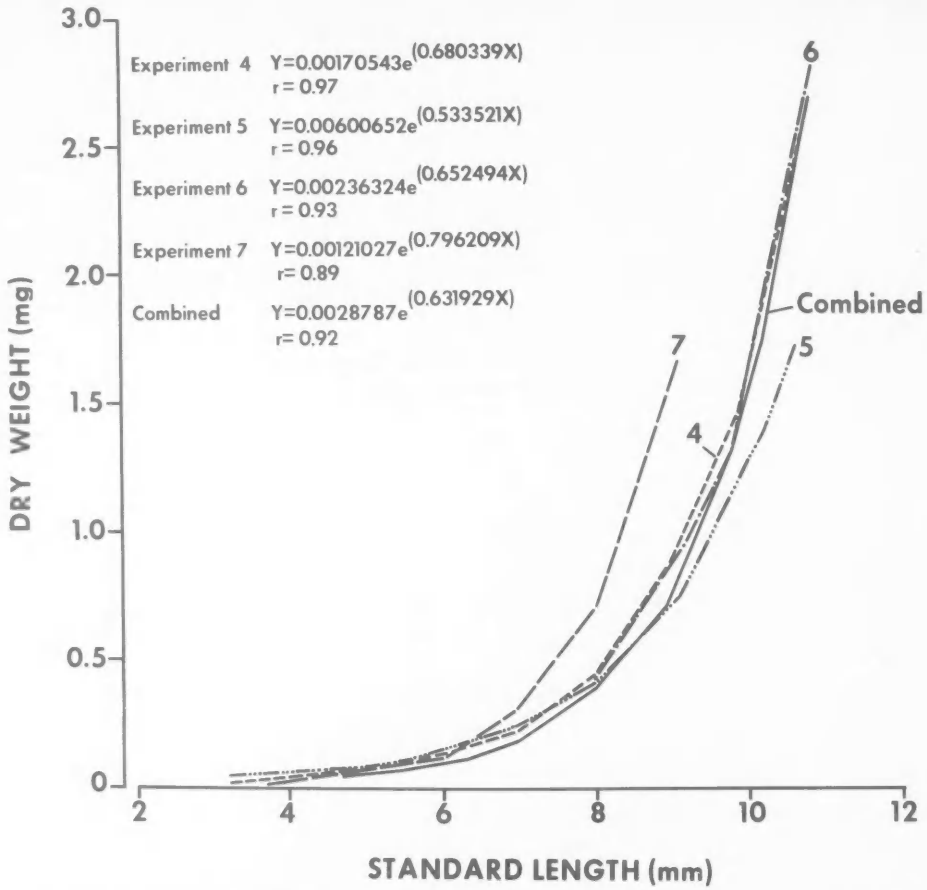

FIGURE 7.—Assimilated tissue dry weights and corresponding standard lengths of four batches of striped bass larvae.

1958; Flüchter and Pandian 1968; Blaxter 1969). Egg size variability was not unexpected as eggs are reported to vary within and among a variety of fish species (*Clupea harengus*, Blaxter and Hempel 1963; *Sardinops caerulea*, Lasker 1962; *Trachurius symmetricus*, Ware 1975; Theilacker 1980[4]).

It appears from studies of embryos and larvae with large oil globules that the energy from the oil is important to larval growth and survival, and the influence of this energy source is present for long periods. In this study and that of Rogers and Westin (1981), striped bass larvae retained their oil energy reserves for extended periods, especially when starved. This is not common in fishes although similar retention of the oil globule was noted in *Bairdiella icistia* (May 1974a) and *Leuresthes tenuis* (May 1971; Ehrlich and Muszuski in press). The oil globule also seemed to help striped bass larvae avoid or prolong the typical point-of-no-return, the time of irreversible starvation (Eldridge et al. 1981). In a review of larval fish physiology, Theilacker (1980) concluded that in addition to egg size and activity, egg lipid level relates most to larval resilience.

[4]Theilacker, G. H. 1980. A review of pelagic larval fish behavior and physiology. Presented at Institute del Mar del Peeru (IMARPE) Workshop, April 21-May 5, 1980.

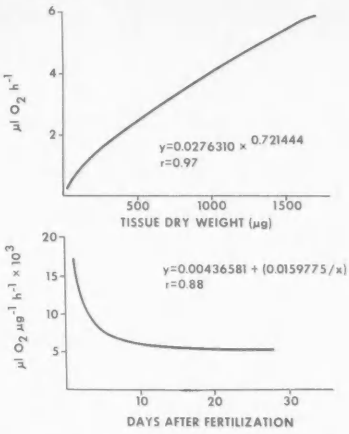

FIGURE 8.—Oxygen consumption of striped bass embryos and larvae plotted against assimilated tissue dry weight (above) and age (below).

In an attempt to compare our laboratory derived estimates of daily food ration with those from wild striped bass larvae we obtained stomach content data of 1,468 field-caught larvae (sized to 11.9 mm SL) spawned from 1971 to 1973. The summarized data of Table 7 show wild larvae were smaller (4.0 to 4.9 mm) than laboratory larvae (6.1 mm) at the time of first feeding. This is possibly due to differences in preservation methods. When wild larvae attained sizes of 7.0 to 7.9 mm, over 75% were feeding. This agrees with our laboratory observation that over 80% of the 2-wk-old and older larvae (>7.0 mm SL) fed actively in food concentrations of 0.50 *Artemia*/ml and greater. The overall average of feeding incidence for wild larvae was 70.5%. Wild larvae also displayed preference for cladocerans, *Cyclops* sp. and *Eurytemora* sp., which, together, accounted for 89% of all food consumed. Other studies of striped bass from east coast nursery areas showed that the largest part of the larval diet consisted of small crustacea and microplankton (Meshaw 1969; Humphries and Cumming 1972).

Using these data we calculated daily caloric rations, according to the previously described formula, for each size category of wild larvae (Table 7). Caloric equivalences for the different food types were obtained from the literature (Richman 1958; Cummins 1967; Clutter and Theilacker 1971; Laurence 1976; Sitts 1978). In-

TABLE 7.—Average feeding incidences, stomach contents by food item, equivalent caloric values, and calculated daily caloric rations of 1,468 striped bass larvae collected in the San Francisco Bay/Delta estuary during 1971-73. The last column presents laboratory-derived average caloric rations for larvae of comparable sizes.

Larval size (mm SL)	% with food in stomachs	Neomysis	Coropium	Cladocerans	Cyclops	Diaptomus	Eurytemora	Acartia	Harpacticoids	Misc. copepods	Total caloric equivalent	Estimated daily ration (cal)	Laboratory derived average ration (cal)
3.0-3.9	0	0	0	0	0	0	0	0	0	0	0		—
4.0-4.9	16.1	0	0.01	0.29	0.18	0	0.24	0.01	0.03	0.01	0.107	0.646	—
5.0-5.9	32.6	0.02	0.09	0.82	0.60	0	0.28	0.01	0.01	0.01	0.299	1.801	—
6.0-6.9	57.5	0	0.10	0.80	0.81	0.01	0.38	0.01	0.01	0.01	0.317	1.910	0.183
7.0-7.9	76.7	0.02	0.11	0.82	1.00	0.01	0.49	0.01	0.02	0.01	0.357	2.152	0.151
8.0-8.9	80.9	0.04	0.14	0.97	1.22	0.01	0.63	0.01	0.02	0.01	0.436	2.627	0.520
9.0-9.9	84.7	0.09	0.18	1.08	1.25	0.01	0.68	0.01	0.03	0.02	0.496	2.989	1.245
10.0-10.9	85.3	0.16	0.22	1.31	1.27	0.04	0.82	0.01	0.01	0.02	0.599	3.609	2.607
11.0-11.9	82.9	0.19	0.28	1.51	1.37	0.02	0.92	0.01	0.02	0.01	0.689	4.151	N/A

formation on natural feeding duration was taken from Miller,[5] which showed that wild larvae feed 24 h a day but feed more intensely during crepuscular periods. Evacuation rate was set at 5 h, a compromise between our estimate of 3.3 h for larvae fed *Artemia* at 18°C and the estimate of 11 to 12 h made by McHugh and Heidinger (1977) for larvae given *Artemia* and held at 25°C. Daily caloric rations for wild larvae range from 0.646 cal for smaller larvae to 4.151 cal for 11.0 to 11.9 mm SL larvae. These rations are higher than those of laboratory larvae. Except for the largest cultured larvae, rations were usually one-half the field larvae rations. Thus within equivalent size categories wild larvae appear to have daily rations substantially greater than those of cultured larvae. Other estimates of daily rations of striped bass larvae range widely. Miller (footnote 5) concluded that field-caught larvae (6.8 to 9.2 mm SL) consumed rations equivalent to 0.159 cal for rotifers or up to 2.958 cal for cladocerans. Doroshev (1970) estimated daily intake of laboratory-reared larvae to be 9.704 to 29.112 cal, consisting of *Cyclops* nauplii or small copepods. Our average calculated daily estimates for the different food concentrations for the 29-d experimental period fall within Miller's estimates of wild larvae (Table 8).

TABLE 8.—Mean daily caloric rations of striped bass larvae given five different food densities from D-7 to D-29.

Food density (*Artemia*/ml)	Mean overall daily caloric ration (calories/larva per d)
0.01	0.035
0.10	0.439
0.50	0.802
1.00	0.823
5.00	1.313

Energy Outputs

Our results suggest that there is compensatory growth in embryos and larvae that offsets initial egg size differences. The size ranges are not as broad in newly hatched larvae and larvae at first feeding (D-7) (seen in Table 5) as they are in the eggs. Likewise, initial egg size corresponds better to the size ranking of larvae at hatching age than it does to larvae at feeding age. The mean instantaneous growth coefficient during the 2-d embryonic period was 1.872 with a coefficient of variation (C.V.) of 8.5% (Table 5). From hatching to first feeding it was 0.647 with a decreased C.V. of 7.0%, an indication of narrowing diversity. Further compensatory growth was seen in tissue weights and standard lengths of feeding larvae (Figs. 4, 5), and convergence of sizes was seen in all food concentrations above 0.10 *Artemia*/ml. Weights were similar on D-25 and lengths on D-27. In the two higher food concentrations, sizes converged by D-17. Compensatory growth was documented years ago in salmon fry (Hayes and Armstrong 1942), so this is not necessarily unique to striped bass. Theilacker (in press) more recently found that growth rates of jack mackerel larvae varied with egg size.

Growth of feeding striped bass larvae was clearly tied to exogenous food consumption as seen in Figure 6. This relation is well established in other larval fishes (O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; May 1974a; Houde 1977; Taniguchi in press).

Growth rates of our larvae, especially those in the higher food concentrations, are similar to findings with other populations of striped bass (Rogers et al. 1977). The most comparable study (Daniel 1976) included continuous introduction of *Artemia* for 10 d in concentrations of 0.004 to 0.030 nauplii/ml. Twenty-five days after hatching larvae grew to an average standard length of 8.5 mm. Fish used in the present study were longer than Daniel's in the two higher food concentrations and smaller in the three lower concentrations. As in our study, Daniel's larvae also grew directly in relation to food density. Tissue weights of Daniel's fish fed the 0.008 and greater *Artemia*/ml concentrations approximated those of our fish fed concentrations of 0.005 and above. Our larvae that fed at 5.0, however, were all heavier than Daniel's larvae. Lal et al. (1977) also cultured California striped bass larvae but in varying salinities. Larvae of comparable age feeding on *Artemia* (densities unreported) were similar to our larvae from the 0.50 nauplii/ml. Larvae from our higher densities were larger.

Oxygen consumption measurements varied directly with size, age, and temperature. Because temperature was held constant in all tests, age and size were the most influential factors affecting oxygen consumption, and these factors produced distinctive patterns. The high metabolic rates (Q_{O_2}'s) demonstrated by embryos and newly hatched larvae were probably the results of the activity accompanying hatching and of the high metabolic needs associated with rapid tis-

[5]Miller, P. E., Jr. 1978. Food habit study of striped bass post yolk-sac larvae. The Johns Hopkins University, Chesapeake Bay Institute, Spec. Rep. 68, Ref. 78-8.

sue growth and differentiation. These needs remained high into the period of feeding transformation and then leveled off to nearly constant rates after D-10. Similar patterns have been seen in other fishes (Smith 1957; Blaxter 1969). The relation of oxygen consumption to weight is usually described in a log-log transformation with a slope approximating 0.8 (Winberg 1956). Our slope of 0.72 shows that our equation describes the weight-metabolism relation up to the final size encountered. Laurence (1977) found winter flounder metabolism profoundly changed after metamorphosis resulting in a curvilinear pattern described best by a third degree polynomial equation. It is likely that striped bass would show similar tendencies when measured further along in development.

Reviews (Blaxter 1969; Eldridge et al. 1977) show that efficiencies during the strictly endogenous energy period of embryos and prefeeding larvae ranged from 40% to 70%. Our findings with striped bass tended toward the low side of this range. *Micropterus salmoides* was most similar to striped bass, with efficiencies of 35.2% to hatching and 43.9% to feeding (Laurence 1969). Like those of striped bass, the eggs of *M. salmoides* also possess large oil globules, and their larvae have similar predatory behavior. Gross growth efficiencies of aquatic consumers in general normally fluctuate between 15% and 35% (Welch 1968). Efficiencies of larval and postlarval fishes have also been found to be within this range (Ivlev 1939a; Laurence 1973, 1977). Ivlev (1945) believed postembryonic stages were restricted to efficiencies <35%, and fish normally have decreasing efficiencies with age (Parker and Larkin 1959; Theilacker footnote 4). All our efficiency values support these conclusions. Whether feeding or not, our older larvae had lower conversion efficiencies, probably resulting from increased metabolic demands associated with greater activity.

All organisms must balance input and output energies to successfully survive, grow, and ultimately reproduce. The essential relations between input and output energies and the equation which balances them have been well discussed by several authors (Winberg 1956; Warren and Davis 1967; Warren 1971; Wiegert 1976). This paper presents data that make up the basic parameters of an energy budget. The basic relation of these components can be presented in:

$$Q_I = Q_W + Q_G + Q_M$$

where Q_I = input energies, whether endogenous, exogenous, or a combination of the two
Q_W = waste energy
Q_G = growth energy
Q_M = metabolic energy.

All but Q_W have been studied by us, and the effects of food density and initial egg size have been discussed. In Figure 9 we present a graphic model of the energy budget of striped bass embryos and larvae fed the high ration diet (5.0 *Artemia*/ml). This model approximates that of Laurence (1977) except that we include input energies of yolk and oil, and we present the relations against time as rates (i.e., calories consumed or expended per 24 h period per organism).

When the energy budget is presented in these terms, some distinctive patterns emerge. Yolk provides a constant energy input until it is exhausted on or about D-7. Oil is used rapidly at first, then more slowly until yolk energy is no longer available and the animal initiates feeding. At this time, the larva increases its use of oil

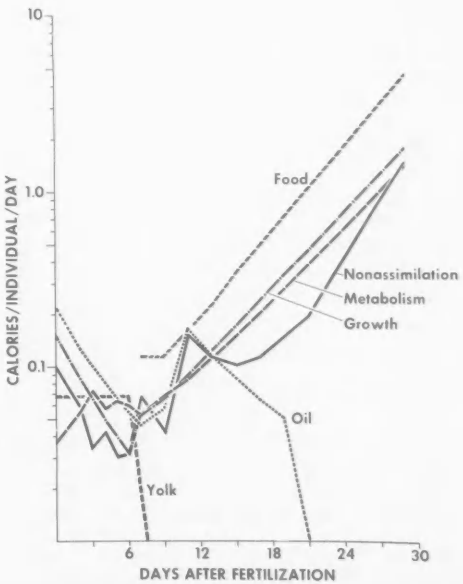

FIGURE 9.—Energy budget of input calories (yolk, oil, and food) and output calories (growth, metabolism, and nonassimilation) presented in calories per individual embryo or larva per day.

until exogenous feeding becomes established, after which it gradually decreases consumption of oil until oil energy is depleted. An initial adjustment to exogenous energy intake is followed by a continuously increasing exogenous input concomitant with decreased reliance on oil energy. Growth showed an interesting pattern that suggested it is closely linked to oil energy prior to feeding and to exogenous food energy after initiation of feeding. Growth rates declined steadily to D-6 and increased abruptly thereafter.

Metabolism increased steadily during incubation and hatching. After the energy consuming hatching process it decreased slightly to the onset of feeding. After D-7, increasing activity associated with feeding resulted in continuously increasing metabolism.

Nonassimilation is the energy remaining after metabolism and growth are subtracted from the total energy input. When energy input is endogenous, nonassimilation comprises poor utilization and/or redeposition of yolk and oil into other tissues. Nonassimilation of exogenous food is mostly due to undigested food. In this model nonassimilation fluctuated with oil input energy and growth to first feeding. It increased during adjustment to feeding and declined when both oil and food calories were available. As *Artemia* became the main energy source nonassimilation increased. Poor digestion in older larvae in the form of nearly intact *Artemia* in the intestines was seen commonly, especially in the high food rations.

The bioenergetics model and its parameters are presently being used to measure various abiotic and biotic stresses, including pollutants. It promises to be a useful method for assessing the effects of these factors.

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STOCK AND RECRUITMENT RELATIONSHIPS IN *PANULIRUS CYGNUS*,[1] THE COMMERCIAL ROCK (SPINY) LOBSTER OF WESTERN AUSTRALIA

G. R. MORGAN,[2] B. F. PHILLIPS,[3] AND L. M. JOLL[4]

ABSTRACT

Abundance of the breeding stock, level of settlement of the puerulus stage, juvenile densities, and recruits to the fishery for *Panulirus cygnus* from 1969 to 1979 are examined.

A dome-shaped relationship between the index of abundance of the breeding stock and subsequent puerulus settlement indicates that stock-dependent effects during the planktonic larval stages apparently control the level of puerulus settlement. However, density-dependent relationships (characterized by more asymptotic relationships between the various life history stages) dominate after settlement of the puerulus on the coastal reefs and control the level of recruitment to the fishery and eventually to the breeding stock. The relationship between the settlement of the puerulus stage and the catch rates of the recruits entering the fishery 4 years later is adequately described by a Ricker's stock-recruitment curve as is the level of puerulus settlement to the subsequent abundance of the breeding stock. The relationship between the level of puerulus settlement and the later abundance of juveniles at various ages is not clear and possible reasons for this are suggested.

The significance of the stock-dependent relationship between breeding stock and puerulus and the density-dependent relationship between puerulus and breeding stock in maintaining recruitment to the fishery is discussed.

The importance of understanding the stock-recruitment relationship in exploited fish populations has been recognized for many years and has been the subject of several workshops and symposia (e.g., Parrish 1973), as well as a great deal of research. While the importance of such relationships in exploited invertebrate stocks has been equally recognized, quantitative data, particularly for crustaceans, has been virtually nonexistent (Hancock 1973).

Like many fish species, crustaceans in general and spiny (rock) lobsters in particular, pass through several distinct stages in their life history and, as Hancock (1973) pointed out, a proper understanding of the overall stock-recruitment relationship can be gained only by considering the relationship between successive stages over a number of years. Hancock's belief is reinforced by the studies of Larkin et al. (1964) and Paulik (1973) who, having considered the theoretical forms of a stock-recruitment relationship involving such multistage life histories, showed that several stable equilibrium points can exist in the overall spawning stock-recruitment curve, depending on the relationships existing between the various life history stages.

The western rock lobster, *Panulirus cygnus* George, the object of an important fishery in Western Australia (Morgan and Barker 1979) passes through several major stages during its life history. These include a series of phyllosoma larvae, a puerulus stage, and juvenile and adult stages. After a planktonic life of 9-11 mo (Chittleborough and Thomas 1969; Phillips et al. 1979), the surviving phyllosoma larvae metamorphose into a puerulus stage and settle between September and January each year in shallow coastal areas. The younger juveniles concentrate on shallow limestone reefs to depths of 10 m, with some larger juveniles to 20 m. At about 4 or 5 yr of age (i.e., 4 or 5 yr from hatching) juveniles migrate from the shallow reef areas onto the continental shelf into depths of 30-150 m where maturity is reached, mating takes place, and the life cycle is completed.

Chittleborough and Phillips (1975) reported that, based on the data available at that time, indices of year-class strengths obtained from the

[1]The western rock lobster is referred to as *P. longipes* or *P. longipes cygnus* in some of the literature quoted; these are synonymous with *P. cygnus*.

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puerulus at settlement and those derived from measurements of density of juveniles of *P. cygnus* aged 2 or 3 yr were consistent. However, they found survival to recruitment into the fishery did not mirror the pattern of year-class strength at or soon after settlement. The purpose of this paper is to examine the changes that take place in the abundance of the various stages in the life history of *P. cygnus* including data on puerulus settlement and juvenile density and to investigate their interrelationships.

METHODS

The abundance of the several stages in the life history of *P. cygnus* has been measured by various methods over a number of years. The methods used have reflected the practical problems of sampling the different stages and have included catch and fishing effort data from the commercial fishery for the adult stage, collectors composed of artificial seaweed to catch the puerulus stage, and mark and recapture studies of the juveniles using baited traps. All ages and year classes referred to in this paper relate to the year of hatching and so include the 9-11 mo larval phase. For example, the 1969 year class was hatched in January-February 1969 and settled as puerulus larvae between September 1969 and January 1970.

Abundance of the Breeding Stock

The western rock lobster is confined to the western coast of Australia from approximately North West Cape to Cape Naturaliste (Fig. 1). The majority of the commercial catch is taken between lat. 28° and 32°S (Sheard 1962). The coastal fishery operates from 15 November to 30 June of the following year although prior to 1978 the coastal season concluded on 14 August each year. The Abrolhos Islands fishing season which extended from 15 March to 14 August prior to 1978, now also ends on 30 June.

The abundance of the breeding stock (i.e., those females carrying external eggs) has been measured since 1966 from research logbook data supplied on a voluntary basis from about 200 boats or 25% of the commercial rock lobster fleet. In addition to catch, fishing effort, and fishing locality information separated into four depth categories, i.e., 0-10, 10-20, 20-30, and over 30 fathoms, each fisherman records his daily catch of numbers of spawning female rock lobsters.

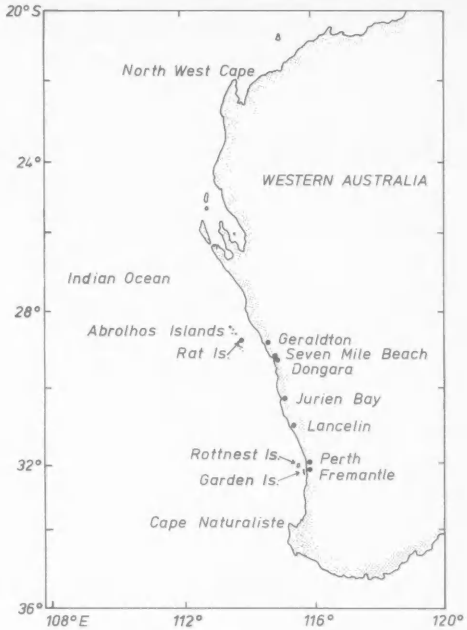

FIGURE 1.—Location of the sites mentioned in the text.

However, these data are not available from the Abrolhos Islands for December, January, and February since this area is closed to commercial fishing at this time each year. Consequently, comparable data on the breeding stock had to be obtained from research vessel cruises to each of the four island groups of the Abrolhos during January and February 1979. Sixty commercial wire beehive pots without escape gaps were set each day for a total of 20 d on the fishing grounds where the greatest concentration of spawning females is to be found. The pots had previously been calibrated in the Garden Island area (Fig. 1) by comparison with commercial catch rates of spawning females. During the comparison, catch rates of spawning females were low (mean of 0.05 animals/pot) and the variances relatively large so it is not surprising that no significant difference (at the 5% level) could be detected between the catch per pot lift of spawning females by the research vessel's pots and the catch per pot lift of spawning females by commercial fishermen's pots. However, additional calibration of the research vessel's pots would add confidence to this conclusion.

Abundance of the Puerulus Stage

Phillips (1972) showed that the last larval stage, the puerulus, of *P. cygnus* could be captured using collectors composed of artificial seaweed moored at the surface within the protection of the coastal reefs. Subsequent studies by Phillips and Hall (1978) have shown that the catches from these collectors provide a measure of the relative strength of settlement from year to year.

All collectors used in this study were as described by Phillips (1972). The collectors were checked monthly after each new moon period when most puerulus settled. All settlement took place at the puerulus stage. The western rock lobsters were removed from the collectors either as puerulus or after they had molted into very small postpuerulus juveniles. Since the planktonic period is 9-11 mo, settlement occurs between September of the year of hatching and the following January.

Abundance of Juveniles

Density of age groups (ages 2-7 yr) has been measured on shallow test reefs at Garden Island (since 1965) and Seven Mile Beach (since 1970), using the single census trap-mark-recapture method described by Chittleborough (1970). These test reefs are adjacent to the collectors used to catch the puerulus stage.

Abundance of Recruits to the Fishery

During late November of each year, large numbers of immature, newly molted, pale colored rock lobsters migrate into deeper water from the shallow water inshore reefs (which are generally inaccessible to fishermen) where they have spent the previous 4 or 5 yr. This offshore movement normally lasts through December and in all lasts about 6 wk. Since they are newly molted, their food requirements are high (Chittleborough 1975) and consequently their catchability by baited pots is high (Morgan 1974). During this migration the fishermen catch large quantities of these animals which are locally known as the "whites" (George 1958). Although a small number of animals undergo two or perhaps three "white" phases in their life cycle, the "white" phase generally occurs only once during an individual's lifetime (George 1958), and this enables the migrating "whites" to be equated with the recruits to the fishery.

Estimates of the abundance of the potential emigrants from the shallow reefs have been made by Chittleborough (1970), although a better measure of their abundance is available from the catch rate (measured as the catch per pot lift) of the commercial fishery during November and December when practically all of the commercial catch consists of "white" rock lobsters. Information on catch and fishing effort for November and December each year has been taken from the fishermen's monthly returns, which are completed as a condition of the fishing license by all fishermen.

RESULTS

Since there have been several customs adopted in the designation of year classes in *P. cygnus* (e.g., Chittleborough 1970; Morgan 1977) a summary of the convention used in this paper will enable the various relationships presented below to be followed more easily. The convention used and the major events in the life history of *P. cygnus* are as follows:

Hatching of eggs	November, December year $x-1$, January, February, and March year x, with midpoint taken as 1 January of year x.
Settlement of puerulus larvae	September year x to January year $x+1$.
Juveniles on inshore reefs	Year $x+1$ to $x+4$ and $x+5$ (ages 1 to 4 or 5).
Migration of "whites" to offshore areas	November and December year $x+4$ and $x+5$, with the majority being $x+4$.
Maturity and first breeding	January and February year $x+6$ and $x+7$, with the majority being $x+6$.

Stock Definition

Based on similarities in catch rates from the commercial fishery, Morgan (1977) concluded that although some population parameters such as growth rates, size at first maturity, etc. varied between localities, the western rock lobster could, as a first approximation, be considered as a single, genetically coherent, unit stock. This view is reinforced by the studies of Phillips et al. (1979) who demonstrated the wide dispersal of

the phyllosoma larvae in the eastern Indian Ocean. Consequently, in the following analyses a single stock has been assumed, although latitudinal differences in some population parameters have necessitated a simple division of the fishery into areas north of lat. 30°S and south of lat. 30°S.

The Breeding Stock

From the research logbook information, it was evident that spawning rock lobsters were concentrated in the 20-30 fathom depth range with an average of 89.9% of the total catch of spawning females each year being taken in this depth range during the period 1966-80. Year-to-year variation was small with the percentage ranging from 86.4% in 1971 to 92.1% in 1967. In addition, the majority of spawning female rock lobsters (average of 81.4% for the period 1966-79) were captured during January and February each year with, again, little year-to-year variation. Accordingly, the catch per pot lift of spawning females taken in 20-30 fathoms in January and February each year has been used as a basis for the calculation of an index of abundance of spawning females. No adjustment for soak time was made since catch per pot lift has been shown to be independent of soak time (Morgan 1977). The use of catch per pot lift data as an index of abundance assumes, of course, that catchability remains constant from year to year. Morgan (1974) has shown that catchability varies during a year in response to molt condition, water temperature, and water salinity. Year-to-year variation in catchability of spawning *P. cygnus* females for January and February is likely to be small, since it would be expected that these animals would be in an intermolt condition, and year-to-year temperature and salinity variation on the spawning grounds in January and February is small (Morgan and Barker 1979).

The average size of the spawning females varies with locality, being larger in southern areas (Morgan and Barker 1979). Average size information on spawning females has been collected on a regular basis since the 1971-72 season from commercial vessels fishing out of the ports of Dongara, Jurien Bay, Lancelin, and Fremantle (Fig. 1). These data have been previously presented in a series of annual reports on the fishery (e.g., Morgan and Barker 1979). Occasional collections of size composition data of spawning females were made prior to the 1971-72 season, particularly at Jurien Bay and Lancelin (B. K. Bowen, unpubl. data). These two sources of data have been used to calculate the average size of spawning female *P. cygnus* for various years. The relationship between size and fecundity (Morgan 1972) has then been used to calculate the number of eggs produced by a spawning female rock lobster of this average size. *Panulirus cygnus* spawns only once per year in most areas in the wild (Morgan 1980b).

Data on the catch rates of spawning female *P. cygnus* taken in 20-30 fathoms in January and February each year, the mean size of these spawning females, and the resultant fecundity are shown in Table 1, separated into two areas: north of lat. 30°S and south of lat. 30°S.

Index of Abundance of Spawning Stock

The most appropriate index of spawning success in *P. cygnus* is the number of first stage phyllosoma larvae released during the hatching period. However, since it has not been possible to measure phyllosoma abundance directly, an indirect measure, utilizing the abundance and fecundity of the spawning females, is necessary. Thus the total number of first stage phyllosoma larvae released is approximately equal to (total number of spawning females) × (their average fecundity).

The number of spawning females in each of the two coastal areas (north and south of lat. 30°S) may be estimated from their catch rate (a measure of density) multiplied by the area of the spawning grounds. The area of the spawning grounds for coastal localities north and south of lat. 30°S is given in Table 2. Thus, for example, a measure of the total number of spawning females north of lat. 30°S in 1966 is given by 0.44 (from Table 1) × 6,690 (from Table 2) = 2,943.6. It should be noted that this measure gives a relative, not an absolute, figure for the numbers of spawning females since a knowledge of the catchability coefficient per unit area, q, would be necessary to convert catch rate (c/g) into absolute numbers (N) by using the relationship

$$c/g = \frac{q \times N}{A}$$

where A = area of the spawning grounds.

Catchability has been measured at the Abrol-

TABLE 1.—Catch (numbers) per pot lift of spawning female *Panulirus cygnus* taken in 20-30 fathoms in January and February each year (c/g), the mean size of the spawning females (S) (in millimeters carapace length), and the resultant fecundity at this size (F), for two coastal areas. The method of calculation of the index of abundance of the breeding stock (I.A.S.) is explained in the text. NA = Not yet available.

	Coastal areas north of lat. 30°S			Coastal areas south of lat. 30°S			All coastal areas	All coastal and Abrolhos areas
Year	c/g	$\bar{S}$ (mm CL)	F	c/g	$\bar{S}$ (mm CL)	F	I.A.S. ($\times 10^7$)	I.A.S. ($\times 10^7$)
1966	0.44			0.53			174	198
1967	0.61	92.2	321,710	0.33			179	204
1968	0.50	90.2	302,110	0.65			205	234
1969	0.49			0.28			146	166
1970	0.40			0.34			136	155
1971	0.23			0.23			84	96
1972	0.48	92.9	328,570	0.16	104.3	440,290	125	143
1973	0.22	90.5	305,050	0.15	104.6	443,230	69	79
1974	0.12	91.3	312,890	0.08	106.4	460,870	37	42
1975	0.14	94.5	344,250	0.13	105.0	447,150	49	56
1976	0.16	93.5	334,450	0.13	104.0	437,350	54	62
1977	0.24	92.0	319,750	0.16	103.9	436,370	75	86
1978	0.24	92.8	327,850	0.11	104.6	443,230	67	76
1979	0.27	NA		0.17	NA		83	95
1980	0.19	NA		0.11	NA		56	64

TABLE 2.—Comparison of egg production estimates for coastal areas north and south of lat. 30°S and the Abrolhos Islands area for 1979.

	Abrolhos	North of lat. 30°S	South of lat. 30°S	Total
Area of spawning grounds from Admiralty charts (km^2) (A)	840	6,690	3,500	11,030
Average size of spawners (mm carapace length (B))	74 (research cruise data)	94 (Morgan and Barker 1979)	105 (Morgan and Barker 1979)	
Fecundity (from Morgan 1972) (C)	143,300	339,300	447,150	
Catch per pot lift of spawning females (D)	1.16 (from research vessel)	0.27 (from fishermen's log books)	0.17 (from fishermen's log books)	
Relative numbers A × D (E)	974	1,906	595	
Egg production × 10^7, E × C (F)	13.99	61.29	26.60	101.88
Percentage egg production	14%	60%	26%	100%

hos Islands (Morgan 1974) but it has not been considered necessary to introduce additional assumptions by converting relative to absolute numbers. From Table 1, it is apparent that for each area the average size of spawning female *P. cygnus* has remained approximately constant for the years for which data are available, although significant differences are apparent between the two coastal areas. Consequently, the mean value of the yearly average sizes for each area has been taken and used to calculate average fecundity for the years 1966-80 using the relationship given by Morgan (1972). These values are north of lat. 30°S, $\overline{CL}$ 92 mm (fecundity 319,750) and south of lat. 30°S, $\overline{CL}$ 105 mm (fecundity 447,150). Calculation of an index of abundance of the spawning stock for each coastal area each year can now be made while summation for each year gives the index for all coastal areas. These are as follows:

North of lat. 30°S: Catch rate × 6,690 × 319,750.
South of lat. 30°S: Catch rate × 3,500 × 447,150.
All coastal areas: Catch rate (north of lat. 30°S) × 6,690 × 319,750 + catch rate (south of lat. 30°S) × 3,500 × 447,150.

Annual indices of abundance of the spawning stock for all coastal areas are shown in Table 1. It should be noted that this is a more refined index than that used by Morgan (1980a).

During the research vessel cruises in the Abrolhos Islands area in January and February 1979, the average catch per pot lift of spawning females was 1.16 or about six times that of coastal areas. However, as shown in Table 2, the small geographical area and the smaller average size of spawning female *P. cygnus* reduces the apparent importance of the Abrolhos Islands area, both in terms of the number of spawning females

and their egg production, when compared with the coastal areas.

The Abrolhos Islands area, therefore, contributed only about 14% of total egg production in 1979. No data on the catch rates of spawning females at the Abrolhos Islands are available for years other than 1979, so it has had to be assumed that the Abrolhos Islands area contributed 14% of the total egg production in each year from 1966, although year-to-year variation in the geographical distribution of settling puerulus larvae will no doubt change this value to some extent. The index of abundance of the spawning stock for all coastal and Abrolhos Islands areas has therefore been estimated by multiplying the coastal index for each year by 1.14. These values are also shown in Table 1.

Abundance of Puerulus Stage

The relative densities of settlement of the puerulus stage (expressed as the mean number per collector settling between September and January at Rat Island (Abrolhos Islands), Seven Mile Beach, Jurien Bay, and Garden Island) are given in Table 3. The data for the different sites have been pooled as an unweighted arithmetic mean and expressed as the mean number of puerulus settling on the collectors, to provide an annual index of settlement.

Abundance of Juveniles

Estimated densities of various year classes at Garden Island and Seven Mile Beach were calculated as described by Chittleborough and Phillips (1975) (Table 4).

Abundance of Recruits to the Fishery

The catch per pot lift of "white" rock lobsters taken during November and December has varied during the years 1964-78 (Table 5) and has resulted in similar variations in total catch from the fishery (Table 6).

The Relationships

Spawning Stock and Puerulus Settlement

Since the peak of puerulus settlement each year occurs from September to January (Phillips and Hall 1978) and is the result of spawning in the previous January and February (Chittleborough and Phillips 1975), the settlement of pueru-

TABLE 3.—Mean number of puerulus settling per collector. — = not measured.

Year of hatching	Index annual settlement	Rat Island	SE	Seven Mile Beach	SE	Jurien Bay	SE	Garden Island	SE
1969	9.7	—		15.2	1.90	4.2	1.07	—	
1970	22.4	[1]35.8	8.94	35.0	2.72	17.8	5.00	0.8	0.85
1971	38.8	47.5	3.12	67.3	5.00	34.7	4.50	2.5	1.90
1972	35.7	68.8	3.90	33.7	3.14	39.6	3.12	0.8	0.85
1973	71.4	73.8	6.07	83.2	4.74	117.4	10.96	11.0	3.06
1974	126.3	130.8	8.83	159.8	12.48	209.6	22.04	5.1	2.55
1975	73.2	105.8	8.60	97.3	6.03	79.6	6.07	10.2	2.25
1976	72.3	106.8	7.09	114.3	7.77	65.6	5.67	2.6	0.81
1977	68.4	112.8	7.85	86.0	7.01	72.2	6.81	2.4	0.60
1978	114.5	182.6	19.33	182.8	11.69	82.4	6.53	10.2	2.59
1979	71.0	102.5	7.42	76.2	4.28	94.4	16.74	11.0	2.67

[1]Converted from two collectors to a different set of four collectors to ensure compatability with later samples.

TABLE 4.—Estimates of year-class strength (no./ha) for juvenile western rock lobsters on nursery reefs (in January). — = not measured; NA = not yet available.

Age (yr)	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Garden Island																
2	—	3,800	4,400	1,400	500	1,200	700	150	1,500	2,600	404	1,932	1,246	2,381	957	1,340
3	3,245	1,070	3,324	317	265	875	537	92	971	1,200	274	1,053	765	969	630	1,300
4	921	810	730	174	195	685	333	60	448	813	149	646	311	638	611	NA
5	697	178	401	128	152	424	217	28	304	443	91	366	205	618	NA	NA
Seven Mile Beach																
2	—	—	—	—	—	—	6,200	6,100	5,100	12,100	11,767	29,869	9,952	5,449	40,163	29,503
3	—	—	—	—	—	5,779	3,825	2,318	2,135	7,591	5,460	4,316	5,012	2,828	6,145	4,986
4	—	—	—	—	—	3,540	1,461	978	1,339	3,522	789	2,174	2,598	433	1,039	NA
5	—	—	—	—	—	1,352	616	613	621	509	397	1,127	397	73	NA	NA

TABLE 5.—Catch (kg) per pot lift of rock lobsters taken by the commercial fishery during November and December for the years 1964-79.

Year	Catch (kg)/pot lift	Year	Catch (kg)/pot lift
1964	1.300	1972	1.057
1965	1.344	1973	0.674
1966	1.352	1974	0.997
1967	1.713	1975	1.115
1968	1.304	1976	1.079
1969	0.973	1977	1.238
1970	1.001	1978	1.443
1971	1.029	1979	1.364

TABLE 6.—Total catch for the western rock lobster fishery.

Season	Total catch ($kg \times 10^6$)	Season	Total catch ($kg \times 10^6$)
1965-66	8.120	1973-74	6.780
1966-67	8.635	1974-75	8.877
1967-68	9.853	1975-76	8.731
1968-69	8.078	1976-77	9.281
1969-70	6.918	1977-78	10.742
1970-71	8.013	1978-79	11.429
1971-72	8.171	1979-80	10.698
1972-73	6.809		

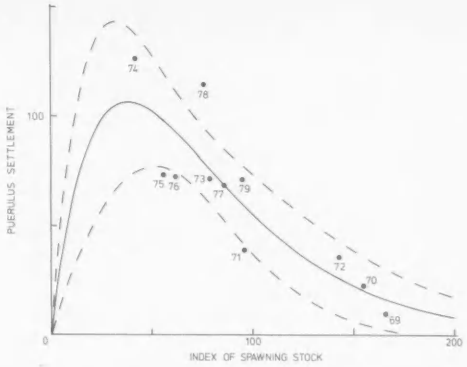

FIGURE 2.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of abundance of spawning *Panulirus cygnus* and the resultant level of settlement of the puerulus stage. The year shown is the season of hatching of the larvae.

lus in year x (plus January of year $x+1$) may be compared directly with the index of abundance of the spawning stock (I.A.S.) in year x.

The Ricker (1958) stock-recruitment relationship of $R = AS\ \exp(-BS)$, where R = recruitment, S = stock size, A = coefficient of density-dependent survival, and B = coefficient of density-independent mortality, was fitted using the method of Cushing and Harris (1973). The relationship is shown in Figure 2 and provides a good fit to the observed data (proportion of sum of squares explained is 0.775). Estimates of A and B with their standard errors (SE) are $A = 7.645$, SE = 2.193 and $B = 0.026$, SE = 0.004.

Puerulus and Juvenile Densities

The relationship between puerulus and juvenile densities is not clear. In contrast to the statement of Chittleborough and Phillips (1975) that puerulus settlement is a good indicator of subsequent juvenile density, the additional data available for Seven Mile Beach (Table 7) indicate that the correlation between puerulus settlement and the subsequent density of 2-yr-old juveniles is poor ($r = 0.359$, $P > 0.05$). Neither do the data give an acceptable fit to a Ricker (1958) stock-recruitment curve. The same conclusion is reached from examination of Garden Island data (Tables 3, 4) ($r = 0.528$, $P > 0.05$). For example, relatively high settlement of puerulus at Seven Mile Beach in 1974 and 1977 (Table 7) when total juvenile density was also high gave rise to very poor and very high densities, respectively, of 2-yr-olds. Beyond 2 yr of age, however, density-dependent mortality is evident. At both Garden Island and Seven Mile Beach there was a significant ($P < 0.001$)

TABLE 7.—Level of puerulus and subsequent juvenile densities of *Panulirus cygnus* in January and mortality rates at Seven Mile Beach, Western Australia. — = not measured; NA = not yet available; arrows connect individual year classes.

Year of hatching	Puerulus mean no. settling/ collector	Age in years of juveniles arising from puerulus				Juveniles present on reef at time of puerulus settlement	Mortality rate/yr of animals aged ≥ 3 yr
		2 No./ha	3 No./ha	4 No./ha	5 No./ha	Total no./ha 2-5 yr	
1969	15.2	6,200	—	—	—	—	—
1970	35.0	6,100	3,825	3,540	—	—	—
1971	67.3	5,100	2,318	1,461	1,352	10,231	0.863
1972	33.7	12,100	2,135	978	616	15,829	0.466
1973	83.2	11,767	7,591	1,339	613	21,310	0.768
1974	159.8	29,869	5,460	3,552	621	39,472	1.934
1975	97.3	9,952	4,316	789	509	15,566	0.686
1976	114.3	5,449	5,012	2,174	397	13,032	0.657
1977	86.0	40,163	2,828	2,598	1,127	46,716	1.879
1978	182.8	29,503	6,145	433	397	36,478	1.780
1979	76.2	NA	4,986	1,039	73	NA	NA

correlation between total density of juveniles on the test reefs and annual mortality rate.

Puerulus Settlement/Juvenile Densities and Recruitment to the Fishery

Chittleborough and Phillips (1975) examined the relationship between the density of larger juveniles on the coastal reefs during the latter part of the year and the success of the commercial white fishery in adjacent waters. They found that, although density-dependent mortality during the juvenile phase ensures reasonably constant recruitment to the fishery over a wide range of initial year-class strengths, in some years the level of puerulus settlement may be inadequate (i.e., below the holding capacity of the shallow-water reefs), and poor recruitment to the fishery may result. They reported that from the data available at that time only the incidence of particularly poor year classes could be used to predict the relative success of the "white" fishery, i.e., to forecast poor future recruitment to the fishery.

Thus, as reported by Hancock (1971), following the low settlement of puerulus larvae on the collectors in 1969-70 (the hatchings of January-March 1969) and low density of early juveniles, it was predicted by Chittleborough and Phillips in 1971 (Anonymous 1974) that low catch levels would be likely in 1972-73 and even lower levels likely at the opening of the 1973-74 season (i.e., the "whites" of November and December 1973). This prediction was borne out by the catches of these 2 years (Anonymous 1974), the white season of 1973 being the poorest on record, particularly in the Fremantle area (reflecting trends observed in the Garden Island research area).

It was pointed out by Chittleborough and Phillips (1975) that the appearance of a very strong settlement, such as that resulting from the hatchings of 1974 at Seven Mile Beach, did not necessarily mean that a high level of recruitment to the fishery could be predicted for the 1977-78 and 1978-79 seasons. The preceding year classes were relatively strong so that the year class of 1974 faced intense competition and high mortality while on the "nursery" reefs. Nevertheless, the 1978 "white" catch rate was the second highest on record.

Figure 3 shows that in fact a good relationship does exist between the level of settlement of the puerulus and the subsequent catch rate (measured as the catch per pot lift) of the "whites" 4 yr later. (Proportion of sum of squares accounted for is 0.574.) The relationship is well described by a Ricker (1958) stock-recruitment curve, fitted by the method of Cushing and Harris (1973). Parameter estimates and their standard errors (SE) are $A = 0.048$, SE $= 0.0066$ and $B = 0.012$, SE $= 0.0018$. A similarly good relationship is achieved by using the puerulus settlement data from Seven Mile Beach only; this is to be expected because of their close correlation with the annual index of settlement ($r = 0.966$, $P<0.01$).

Since the "whites" catch contributes about 40% of the total catch of any one season, it follows from Figure 3 that there should also be a good relationship between the level of puerulus settlement in year x and the total commercial catch rate of the season beginning in November, year $x + 4$, despite the inevitable confusion of year classes in catches taken after December (i.e., after the "whites") each season. The total commercial catches for 1965-66 to 1978-79 are shown in Table 6. The influence of the poor white catch rate of 1973 and the high white catch rate of 1978 on total catches of these years can be clearly seen.

Puerulus Settlement and Subsequent Spawning Stock

Whereas the relationships between the other stages in the life history of *P. cygnus* are not influenced by the effects of fishing mortality, the rela-

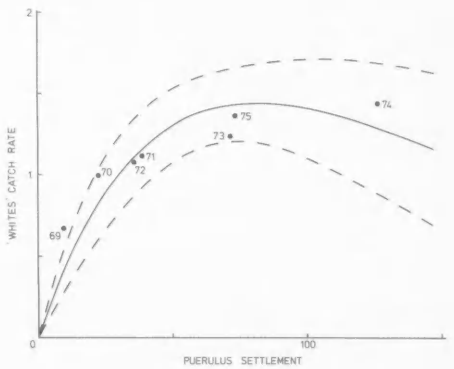

FIGURE 3.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of the annual level of puerulus settlement and subsequent catch rates of *Panulirus cygnus* at recruitment into the fishery 4 yr later. The year shown is the season of hatching of the larvae.

tionship between puerulus settlement and the subsequent spawning stock will inevitably be confused by the effects of variable amounts of fishing pressure on the commercial stocks between the time the rock lobsters are recruited to the fishery as whites and the time that they become mature. In addition, the mature females will be subjected to fishing pressure when they are not carrying eggs. When they are carrying eggs, the fishermen are required by law to return these mature females to the sea.

This fishing pressure on the mature and immature stocks will lead to a reduction in the abundance of the spawning females compared with their potential abundance if there was no fishing pressure. Moreover, the degree of reduction will be a function of the fishing effort (f) since

$$N_t = N_0 e^{-(M+qf)t}$$

where N_t = numbers present at time t
N_0 = numbers present at time 0
M = instantaneous natural mortality rate
q = catchability coefficient.

If the growth rate of *P. cygnus* is considered (Morgan 1977), it will take approximately 1 yr in coastal areas north of lat. 30°S for female rock lobsters to grow from the legal minimum length of 76 mm to the average size of a mature female of 92 mm (Table 1) and approximately 2 yr in areas south of lat. 30°S to grow from 76 mm to the average size of a mature female of 105 mm. Therefore, as a first approximation and neglecting the apparently small influence of the Abrolhos Islands area, it will be assumed that female *P. cygnus* are subjected to fishing pressure for an average of 1.5 yr during their life in the fishery. The indices of abundance of the spawning stock for all areas (Table 1) can now be adjusted to take into account the probable effects of fishing pressure by assuming the index for any year, i, is not only a result of puerulus settlement in previous years but has been reduced by the effect of fishing effort in year $(i-1)$ and one-half the fishing effort in year $(i-2)$.

Using the effective fishing effort data given by Morgan (1979) and Hancock (1981), a relative index, R.I., for later years can be calculated so that it takes into account the effects of fishing effort prior to maturity. This will be given by

$$\text{R.I.}\ (i) = \text{I.A.S.}(i)/\exp\ (-q(f(i-1) + 0.5\, f(i-2)))$$

where $f(i-1)$ = fishing effort in year $i-1$
$f(i-2)$ = fishing effort in year $i-2$
I.A.S.(i) = index of abundance of the breeding stock in year i.

Using the values of fishing mortality rate F and effective effort, f, given by Morgan (1977) a value of q may be calculated from

$$q = \frac{F}{f}.$$

This gives an average value of q for the period 1967-73 of 1.4×10^{-7}.

Using the above formula and value of q, relative indices of abundance have been calculated and are shown in Table 8.

The spawning stock will inevitably comprise a number of year classes each of which is the result of puerulus settlement some 6 yr earlier. However, at the high levels of fishing effort which have been characteristic of the fishery in recent years (Morgan 1979) the breeding stock will be dominated by the younger year classes. Using the value of q of 1.4×10^{-7} and the value of the natural mortality rate M of 0.226 (Morgan 1977), it can readily be shown that during the 1978-79 season, the total instantaneous mortality rate Z was about 1.54. At this level of mortality, only about 21% of spawning females may be expected to survive for a second year's spawning and about 5% for a third year.

The relative indices of the spawning stock

TABLE 8.—The relative index of the breeding stock (R.I.) calculated from the index of abundance of the breeding stock (I.A.S.), and adjusted for fishing effort. The method of calculation is explained in the text. NA = not yet available.

Fishing season	I.A.S. ($\times 10^7$) from Table 1	Fishing effort ($\times 10^8$)	R.I. ($\times 10^7$)
1963-64		4.798 (assumed)	
1964-65		4.798	
1965-66	198	5.036	542
1966-67	204	5.147	578
1967-68	234	5.173	684
1968-69	166	4.292	491
1969-70	155	5.771	406
1970-71	96	7.888	291
1971-72	143	7.536	646
1972-73	79	7.253	394
1973-74	42	7.127	196
1974-75	56	8.035	252
1975-76	62	8.100	314
1976-77	86	8.339	469
1977-78	76	9.765	431
1978-79	95	9.357	668
1979-80	64	NA	470

shown in Table 8 will therefore represent a majority of 6-yr-old spawning females with relatively minor contributions from older year classes. The relative index (R.I.) of the spawning stock may then be directly related to the puerulus settlement 6 yr earlier. This relationship is shown in Figure 4 where again, a Ricker (1958) stock-recruitment relationship provides a good description of the data. (Proportion of sum of squares accounted for is 0.845.) Parameter estimates and their standard errors (SE) are $A = 21.17$, SE $= 2.43$ and $B = 0.013$, SE $= 0.0016$. This relationship however may be less apparent at lower levels of fishing effort where the spawning stock would not be so dominated by the younger year classes.

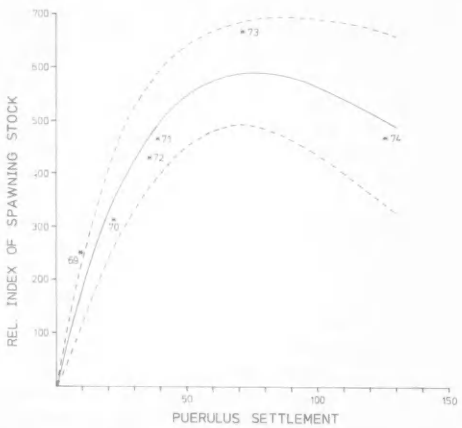

FIGURE 4.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of the annual level of puerulus settlement and subsequent relative abundance of the breeding stock (i.e., adjusted to the same level of fishing effort as explained in the text) of *Panulirus cygnus*. The year shown is the season of hatching of the larvae.

DISCUSSION

During the period 1969-79, it has been possible to measure abundance of the various life history stages of the rock lobster *P. cygnus* using a variety of methods. The subsequent preliminary analysis of the interrelationships, shown in Figures 2-4 and Table 7, has provided information both on the regulatory strategies of the *P. cygnus* population and on the effect of fishing pressure on the stocks.

A dome-shaped relationship is apparent in Figure 2 which is indicative of strong stock-dependent effects (following the terminology of Harris 1975) operating during the planktonic larval stages of *P. cygnus*. This results in the greatest abundance of puerulus being produced by an initially small number of spawning females and a very much lower abundance of puerulus being produced by a large number of spawning females. Cushing (1971) and Cushing and Harris (1973) have shown that such dome-shaped relationships are characteristic of fish with high fecundities, whereas those with low fecundities have more asymptotic relationships. In this respect, the western rock lobster is highly fecund (Morgan 1972), a characteristic which confers upon the species a greater capacity for stabilization and resistance to environmental perturbations. The mechanism by which this stock-dependent mortality occurs is not known, although Harris (1975) and Cushing and Horwood (1977) have shown that such pronounced dome-shaped stock-recruitment relationships can only occur when the number of predators (or cannibals) is explicitly related to the number of eggs or larvae released. Chittleborough (1979) suggested that low levels of zooplankton off the west coast of Australia impose density-dependent (stock-dependent in Harris terminology) mortality upon *P. cygnus* larvae.

Once the puerulus have settled in the coastal reef systems, more asymptotic relationships are apparent which are indicative of density-dependent, rather than stock-dependent, processes (Harris 1975). This results in more asymptotic relationships between the level of puerulus settlement and the subsequent abundance of recruits to the fishery (Fig. 3) and to the breeding stock (Fig. 4). The intermediate relationship between the level of puerulus settlement and the abundance of juveniles of various ages (Table 7) does not appear to be as clear. This may be a result of the juvenile abundance being measured on small areas of reef which may, or may not, be representative of the abundance of juveniles over a wider area. It is possible, at times of high puerulus settlement, that reef areas underutilized or not normally used by juveniles may be occupied. Alternatively the area available to juveniles for either shelter or food supply may vary over a period of years because of changing reef siltation or seagrass bed development. Dramatic changes in reef occupancy by juvenile and adult *Panulirus homarus homarus* (Linnaeus) caused by siltation have been observed at Durban in South

Africa by Smale (1978), and similarly Booth (1979) suggested that varying survival and possible changes in location of juveniles may occur in *Jasus edwardsii* (Hutton) at Castlepoint in New Zealand as a result of periodic sand movement in the area. Chittleborough (1975) has pointed out that the availability of food on the coastal reefs is probably the predominant factor limiting the survival of juveniles. Studies in progress should provide further data to examine this hypothesis. The role of competitors and predators also requires further examination.

Because of the close relationship between the level of puerulus settlement and subsequent abundance of recruits to the fishery, the level of puerulus settlement can be taken as an indicator of the likely level of the future fishery. The data for Seven Mile Beach, which is near the center of the range of population, appears to provide a satisfactory basis for this prediction up to the present time. However, its use as the sole measure of puerulus settlement would introduce assumptions regarding the future puerulus distribution. The densities of juveniles on small test reefs do not appear at this time to provide a good basis for estimation of the future recruitment to the fishery.

The combination of a stock-dependent relationship between breeding stock and puerulus settlement and a density-dependent relationship between puerulus and breeding stock will result in a population which has only one stable equilibrium point of abundance (Paulik 1973), the location of this point being dependent upon the fishing mortality rate on spawning and prespawning animals. If fishing effort is high the number of spawning female rock lobsters will be reduced, which, from Figure 2, will lead to a higher level of puerulus settlement. This higher level of puerulus settlement will then result in a good recruitment of "whites" to the fishery. The possibility of incorporating the relationships between these various life history stages into a production model of the fishery is therefore feasible and warrants further investigation. However since the results presented here are preliminary, in the sense that a longer time series of data would be needed to add confidence to the relationships shown in Figures 2-4, such a production model may at present be premature.

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SPAWNING, AGE DETERMINATION, LONGEVITY, AND MORTALITY OF THE SILVER SEATROUT, *CYNOSCION NOTHUS*, IN THE GULF OF MEXICO[1, 2]

DOUGLAS A. DEVRIES[3] AND MARK E. CHITTENDEN, JR.[4]

ABSTRACT

Cynoscion nothus females from the Gulf of Mexico off Texas matured at 140-170 mm SL as they approached age I. Spawning occurred from early May through late October but primarily in two periods, May and August-September. Greatest spawning occurred in the August-September period when two distinct spawned groups (intrayear class cohorts) were produced. The multiple-spawned group structure within a year class may be important to the population dynamics and stability of *C. nothus*. This species reached 130-190 mm SL at age I. Only one year class occurred or dominated in any one month, and only two year classes were ever present at once. The largest specimen captured was 190 mm SL, and 99% were <160 mm. The maximum life span (t_L) was only 1-1.5 years off Texas but might be 2 years in the northcentral gulf. The total annual mortality rate was best estimated at 99.83% and probably is no lower than 90% if the life span is as long as 2 years. Larger *C. nothus* almost disappeared during winter suggesting an offshore movement for overwintering.

The silver seatrout, *Cynoscion nothus*, smallest of four congeners found along the U.S. Atlantic coast, ranges from Chesapeake Bay to the Bay of Campeche (Hildebrand and Schroeder 1928; Hildebrand 1955). *Cynoscion nothus* is one of the more abundant fishes of the nearshore waters of the northern Gulf of Mexico (Hildebrand 1954; Moore et al. 1970; Gutherz et al. 1975). It is not considered an estuarine species (Ginsburg 1931; Hildebrand and Cable 1934), but small numbers of *C. nothus* have been taken in bays throughout the year (e.g., Gunter 1938, 1945; Swingle 1971; Dahlberg 1972).

Despite its abundance, no published study has been directed at *C. nothus* in the gulf. Little is known about its life history, although Mahood (1974) described spawning and monthly size composition in Georgia waters. General notes on *C. nothus* appear in many faunal studies, including Hildebrand and Cable (1934), Gunter (1938, 1945), Chittenden and McEachran (1976), and in a literature review by Guest and Gunter (1958).

This paper describes age determination for silver seatrout, spawning seasonality and periodicity, growth, mortality, diel changes in availability, and total weight-standard length, girth-standard length, and standard length-total length relationships.

METHODS

Collections were made monthly from February through December 1977 and in March 1978 in the Gulf off Port Aransas, Tex., aboard the Texas Parks and Wildlife Department's RV *Western Gulf*, using a 13.7 m otter trawl with 5.1 cm stretched mesh in the cod end. Stations were usually occupied at 11 m depth at night and at 7, 15, and 18-24 m during the day. Additional night collections were made from May through October 1977 at 20-22, 29-31, and 38 m.

Cynoscion spp. were fixed in 10% Formalin[5] and transferred to 40% isopropanol before processing. *Cynoscion nothus* were separated from *C. arenarius* primarily by comparing the anal fin base to the eye width, a procedure based on the comparatively low anal fin ray counts and larger eye size that Ginsburg (1929) reported in *C. nothus*. The anal fin width equals or is only slightly greater than eye width in *C. nothus*, but

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[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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it is about 1.5-2 times the eye width in *C. arenarius*. Standard length (SL) was measured on all fish captured off Port Aransas. A random number table was used to select 300 specimens each month for intensive processing to determine age, total weight (TW), standard length, girth (G) at the anterior origin of the dorsal fin, sex, gonad weight to the nearest 0.1 g, and gonad maturity stage. All specimens were processed if <300 were collected in any month, and all fish larger than the following sizes were processed: 150 mm SL in April, 75 mm in September, 75 mm in October, 150 mm in November, and 110 mm in December. Maturity stages were assigned to immature and female fish (Table 1) using a slight modification of Kesteven's system (Bagenal and Braum 1971). Scales were taken above the lateral line over the anal fin, where they normally persisted. Cellulose acetate impressions were examined, using a scale projector initially, but a dissecting microscope was employed for a second reading made a year later. No scales were taken from fish <60 mm SL. Annuli were identified knowing the size and collection date of each fish and using standard criteria (Tesch 1971) and procedures used for *C. nebulosus* and *C. regalis* (Klima and Tabb 1959; Tabb 1961; Massman 1963; Merriner 1973). Specific characters used to identify annuli included 1) a definite clear zone between circuli in the anterior field (Fig. 1), 2) appearance of secondary radii *in conjunction with* the clear zone, 3) cutting over of circuli in the lateral field, and 4) appearance of these characters on all or most scales examined. Marks interpreted as false annuli appeared on only a few scales from a fish, usually lacked cutting over, or lacked a clear zone between circuli in conjunction with secondary radii.

Additional specimens were collected monthly from October 1977 through July 1978 off Freeport, Tex., using double-rigged 10.4 m (34 ft) shrimp trawls with 4.4 cm stretched cod end mesh. These collections were made during the day at 7-9, 11, 15-17, 18, 27, 37, and 46 m. Total length (TL) was measured on all fish captured and converted to standard length, using regression relationships presented herein. These length frequencies were used to support findings based on collections off Port Aransas.

Spawned group identities (intrayear class cohorts) within each year class were indicated by specifying the year and probable month when they hatched, e.g., August$_{76}$. Spawning periodicity and group identities assume that a 30 mm TL

TABLE 1.—Description of gonad maturity stages assigned to *C. nothus*.

Stage	Description
Immature	Gonads not visible or barely visible, sexes indistinguishable.
Maturing virgin	Gonads visible but very small, sexes indistinguishable to naked eye.
Early developing	Ovaries small, reddish, occupy 10% or less of body cavity, individual eggs not visible to naked eye.
Late developing	Ovaries orangish yellow, extend length of body cavity and occupy 25-50% of it, opaque eggs clearly discernible to naked eye.
Gravid	Ovaries occupy 50% or more of body cavity, up to half the eggs translucent.
Ripe	Ovaries fill over half the body cavity, no fat along inner margins of ovaries, over half the eggs translucent.
Spawning/spent	Ovary flaccid, partially or completely empty, no opaque eggs.
Resting	Ovaries small but distinguishable in fish large enough to be mature.

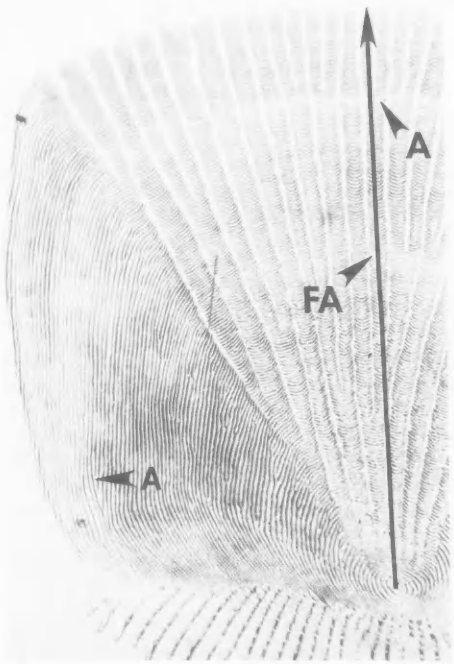

FIGURE 1.—Scale from a 177 mm SL *C. nothus* captured in June showing one annulus (A). The annulus is identified by cutting over in the lateral field and secondary radii in conjunction with a clear zone between circuli. A false annulus (FA) lacks cutting over and was absent on several scales. The axis depicted by the long arrow indicates where scale measurements were made.

(about 21 mm SL) at 1 mo of age for *C. regalis* (Welsh and Breder 1923) can be extrapolated to *C. nothus*. Size descriptions of spawned groups (Table 2) were based upon major portions of specific frequency distributions cited; approximate modes and/or midranges were used to describe central tendency as judged best, often ignoring extreme sizes. Ages when spawned groups disappeared (Table 3) assume hatching at the beginning of months specified in the group identity. Maximum life span was approximated in the sense of the Beverton-Holt model parameter t_L (Gulland 1969) following Alverson and Carney's (1975) definition that only about 0.5-1% of the catch exceeds age t_L or its corresponding lengths.

RESULTS

Spawning

Cynoscion nothus mature at 140-170 mm SL as

TABLE 2.—Growth data for spawned groups of *C. nothus* from the Gulf of Mexico off Port Aransas and Freeport, Tex. Unadjusted growth increments between indicated collection dates were converted to growth/30 d and plotted in Figure 7. Blank spaces in columns for modes and growth increments represent instances in which we consider size data (Figs. 3, 4) too unclear to warrant further analysis.

Spawned group and collection date	Age (mo)	Size range (mm SL)	Mode (M) or midrange (MR) (mm SL)	Unadjusted growth increment (mm SL)
		PORT ARANSAS		
September$_{77}$				
10-11 Nov. 77	2	30-60	47	8
1 Dec. 77	3	40-75	55	
August-September$_{76}$				
9 Feb. 77	5-6	40-75	49 (M)/57 (MR)	8 (M)/8 (MR)
14, 29 Mar. 77	6½-7½	40-90	57 (M)/65 (MR)	7 (M)/8 (MR)
5-6 Apr. 77	7-8	45-100	64 (M)/73 (MR)	30 (MR)
22-26 May 77	9-10	85-120	103 (MR)	20 (MR)
29-30 June 77	10-11	105-140	123 (MR)	27 (MR)
19 July 77	10½-11½	130-170	150 (MR)	
August-September$_{77}$				
8 Mar. 78	6-7	45-115		
May$_{76}$				
5-6 Apr. 77	11	130-160		
22-26 May 77	12½-13	155-170		
7 June 77	13	155-180		
29-30 June 77	14	160-185		
May$_{77}$				
19 July 77	2½	52-61		
2 Aug. 77	3	78		
20-28 Sept. 77	4½	70-115		
5 Oct. 77	5	80-125		
10-11 Nov. 77	6	100-155		
1 Dec. 77	7	115-150		
August$_{77}$				
20-28 Sept. 77	1½	25-70	41 (M)	15
5 Oct. 77	2	35-85	56 (M)	21
10-11 Nov. 77	3	55-100	77 (M)	18
1 Dec. 77	4	75-115	95 (M)	
		FREEPORT		
September$_{77}$				
5 Nov. 77	2	22-55	40 (M)	10
2-3 Dec. 77	3	25-75	50 (M)	
August-September$_{77}$				
19-20 Feb. 78	5½-6½	48-110	79 (MR)	
21-22 Mar. 78	6½-7½	42-112	77 (MR)/42 (L)	13 (MR)/13 (L)
14-15 Apr. 78	7½-8½	55-125	90 (MR)/55 (L)	7 (MR)/17 (L)
8-9 May 78	8½-9½	72-122	97 (MR)/72 (L)	25 (MR)/26 (L)
14-15 June 78	9½-10½	98-145	122 (MR)/98 (L)	25 (MR)/27 (L)
15-16 July 78	10½-11½	125-168	147 (MR)/125 (L)	
May$_{77}$				
1 Oct. 77	5	90-140		
5 Nov. 77	6	125-160		
14-15 Apr. 78	11½	140-160		
8-9 May 78	12	160-190		
14-15 June 78	13½	165-185		
August$_{77}$				
1 Oct. 77	2	25-85	55 (MR)	30
5 Nov. 77	3	55-110	85 (M)	5
2-3 Dec. 77	4	70-118+	90 (M)	

TABLE 3.—Periods of time, sizes, and ages when spawned groups of *C. nothus* were last captured off Port Aransas and Freeport, Tex.

Spawned group and location	Period	Size (mm SL)	Age (mo)	Comments
Aug.-Sept. 76				
Port Aransas	20, 21, 28 Sept. 77	150-190	12-13	A few specimens of uncertain ID in Nov. 77 may be 14-15 mo.
Freeport	5 Nov. 77	160-190	14-15	A few specimens of uncertain ID may belong to this month class.
May 76				
Port Aransas	29, 30 June 77	160-185	13	ID and sizes unclear
May 77				
Port Aransas	1 Dec. 77	115-150	7	A few specimens of uncertain ID in Mar. 78 may be 10 mo.
Freeport	14-15 June 78	165-185	13	ID and sizes unclear
Aug. 77				
Port Aransas	1 Dec. 77	75-115	4	Group not distinct after Dec. 77
Freeport	2, 3 Dec. 77	70-118	4	Group not distinct after Dec. 77
Sept. 77				
Port Aransas	1 Dec. 77	40-75	3	Group not distinct after Dec. 77
Freeport	2, 3 Dec. 77	25-75	3	Group not distinct after Dec. 77
Aug.-Sept. 77				
Port Aransas	8 Mar. 78	45-115	6-7	Still dominant in last collection
Freeport	15, 16 July 78	125-168	10-11	Still dominant in last collection

they approach age I. Many females were classified as early developing at 100-135 mm SL (Fig. 2). Most of the 15 fish classified as ripe or gravid were 140-170 mm SL. Age compositions and sizes at age presented later indicate that *C. nothus* mature to first spawn at 12 mo.

Silver seatrout in the northern gulf spawn from early May through late October. The collection of fish 45-55 mm SL in late June and 50-60 mm in mid-July indicates that spawning begins by early May off Port Aransas (Fig. 3). Spawning must have continued to late October, because fish 25-30 mm SL were collected from mid-August through early December. It appears that no spawning occurred from November through March or April because we captured no fish <40 mm SL after early December, and the smallest fish from February to May (Figs. 3, 4) belong to groups that were hatched before November and continued to grow through the winter.

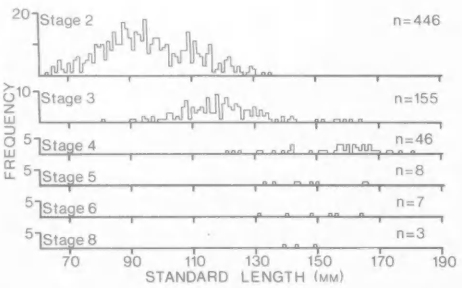

FIGURE 2.—Sizes of immature and female *C. nothus* in maturity stages two through eight. Maturity stages are 2) maturing virgin, 3) early developing, 4) late developing, 5) gravid, 6) ripe, 7) spawning/spent, and 8) resting. No stage 7 fish were caught.

Spawning occurs in two main periods each year—spring and late summer—and within each year class may produce at least three intrayear class cohorts or spawned groups, two of which may be produced in the late summer period. This is indicated by the polymodal length frequencies of fish collected off both Port Aransas (Fig. 3) and Freeport (Fig. 4), a pattern also evident in a reanalysis of Chittenden and McEachran's (1976, fig. 10) data from mid-January 1974 (Fig. 5). The polymodal frequencies do not reflect individual year classes nor do they reflect changes in size with depth. The length-frequency modes represent spawned groups that can be traced readily as follows: 1) The August$_{77}$ and September$_{77}$ groups off Freeport and Port Aransas in the period September-December 1977, 2) the August-September$_{76}$ and August-September$_{77}$ groups, which represent composites of the two individual spawned groups, in the periods February-July 1977 off Port Aransas, March 1978 off Port Aransas, and February-July 1978 off Freeport, and 3) the less distinct modes which we interpret as May$_{76}$ and May$_{77}$ groups in the periods April-June and September-December 1977 off Port Aransas and October 1977-May 1978 off Freeport. The identity of a distinct group 95-130 mm SL off Port Aransas in August 1977 is not certain. It might have hatched in spring 1977, or more probably represents survivors of the August-September$_{76}$ group. Similarly, the identity

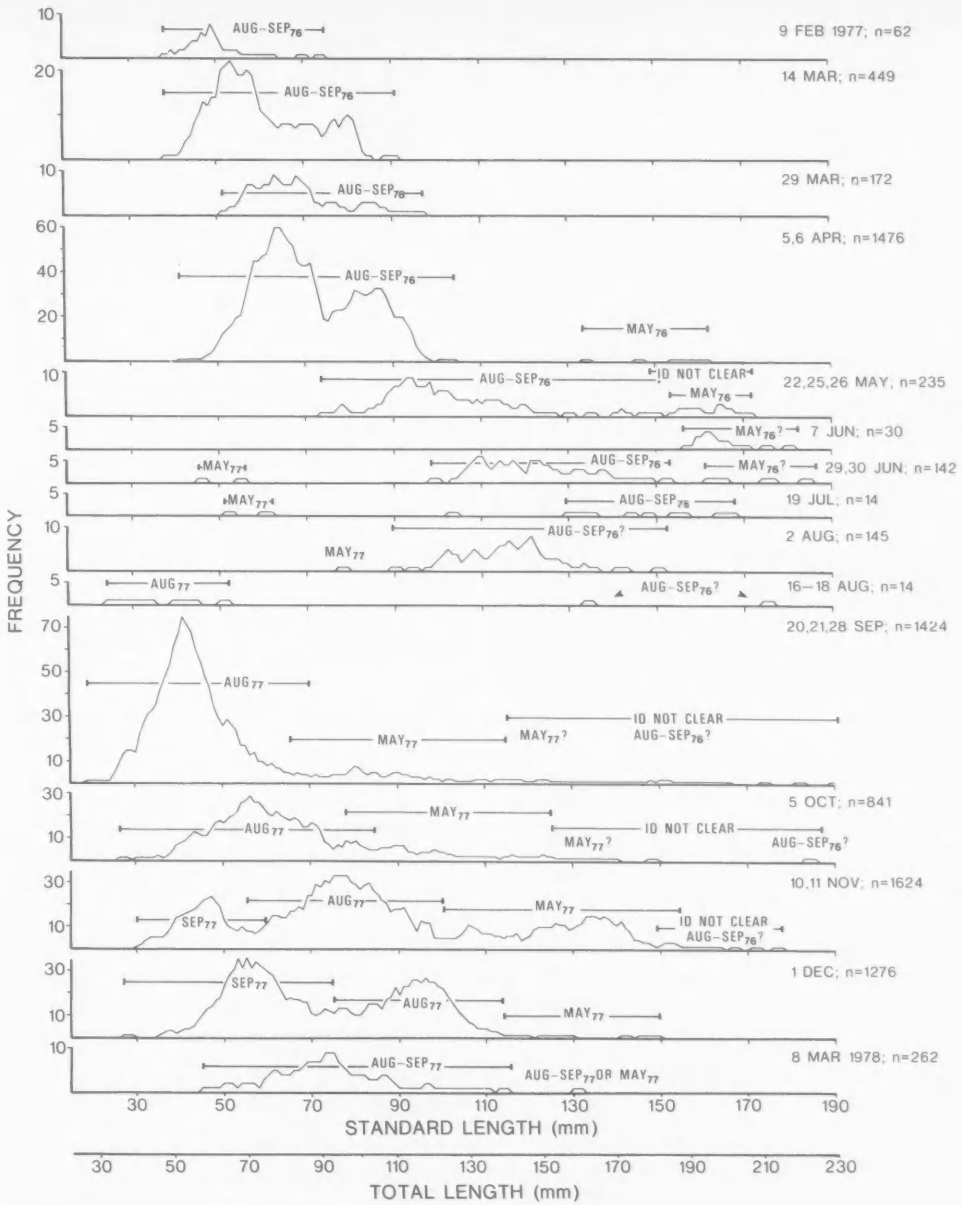

FIGURE 3.—Monthly length frequencies (moving averages of three) of *C. nothus* captured off Port Aransas. Group identity (ID) often is not clear where spawned groups meet.

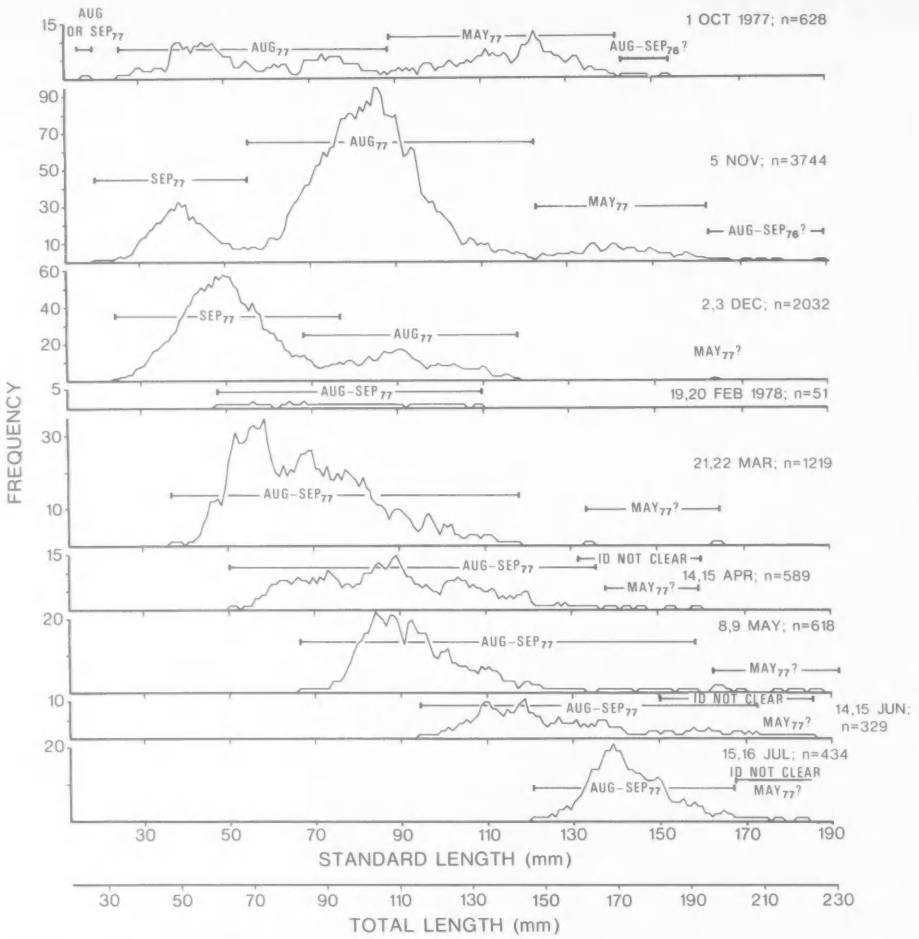

FIGURE 4.—Monthly length frequencies (moving averages of three) of *C. nothus* captured off Freeport. Group identity (ID) often is not clear where spawned groups meet.

of most large individuals off Port Aransas in fall 1977 is not certain.

Greatest or most successful spawning occurs during late summer. Many fish 25-65 mm SL were taken at 11, 12, and 29 m off Port Aransas in late September (August$_{77}$ group in Figure 3). This August-spawned group was collected at widely separated locations and formed a principal mode off Port Arnasas through early December. Fish of this size also formed a dominant mode off Freeport from October through December (August$_{77}$ group in Figure 4). Similarly, a group hatched in September formed a principal mode off Port Aransas and Freeport during November and December (September$_{77}$ group in Figures 3, 4). In contrast to these late summer groups, fish hatched in late spring did not form dominant modes.

Gonad maturity data suggest that *C. nothus* spawns from May through September in agreement with the spawning season indicated by length frequencies. Gravid or ripe females were

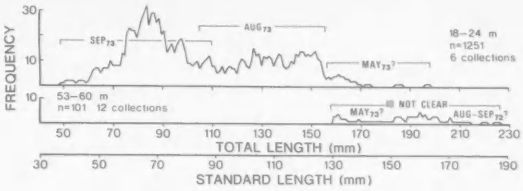

FIGURE 5.—Length frequencies (moving averages of three) of *C. nothus* captured off Freeport, Tex., 6-15 January 1974, by depth. Frequencies were reanalyzed from Chittenden and McEachran (1976, fig. 10). Group identity often is not clear where spawned groups meet.

captured during late May, June, and late September (Fig. 6), and other females 130 mm SL or larger were in the late developing stage. Some males had large gonads from May through September, and running ripe males were captured off Freeport in June and off Port Aransas in September. Females were only in the developing and resting stages in November and December, and no large females were captured from February through April.

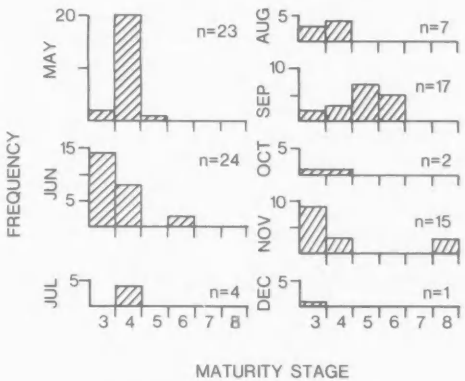

FIGURE 6.—Monthly maturity stages of female *C. nothus*. Maturity stages are 3) early developing, 4) late developing, 5) gravid, 6) ripe, 7) spawning/spent, and 8) resting.

Growth and Age Determination by Length Frequency

Only one year class of *C. nothus* occurred or dominated in any 1 mo. Fish of the 1976 and 1977 year classes occurred off Port Aransas during June, July, and August 1977 (Fig. 3). These were the only months when two year classes were clearly evident, although the comparatively few large individuals of uncertain identity in September-October 1977 probably were of a second year class. Only the 1976 and 1977 year classes occurred off Freeport from October 1977 through July 1978, but the comparatively few individuals of the 1976 year class appeared only in October and November (Fig. 4).

Cynoscion nothus reached 130-190 mm SL at age I. Fish of the dominant August and September spawned groups averaged 145-150 mm SL at 11 mo, although individuals ranged from 125 to 170 mm SL (Table 2). Similarly, the few survivors of the May groups were 130-190 mm SL at 11-14 mo. These observed sizes at age agree with the mean back-calculated length of 156 mm SL presented later.

Growth increments varied between months. The August and September spawned groups grew fastest in June and September, averaging about 25-30 mm SL/30 d (Fig. 7). Growth of recently hatched young steadily decreased from October to December and was smallest during the December-March period when increments averaged 5 mm SL/30 d. Growth increments then steadily increased to about 15-20 mm SL/30 d from March to June. The apparent pattern of greatest growth during the warm months and slowed growth during winter might be misleading. We have no growth data for the late summer period when the August-September groups

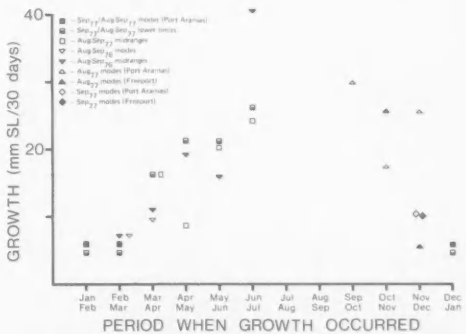

FIGURE 7.—Monthly growth increments of *C. nothus*. Unadjusted growth increments (Table 2) were adjusted to growth/30 d.

would have spawned. Growth from July through September could have been high as the apparent pattern suggests, or it might have slowed down and/or ceased as these fish matured and spawned.

Age Determination Using Scales

Silver seatrout can be aged using scales, although few fish had scales with either an annulus or false annulus. Only 38 of 1,483 fish (2.6%) had an annulus, and no fish had more than one. Only 41 fish (2.8%) had a false annulus, and they included 5 fish with an annulus. These percentages overemphasize the frequency of annuli and false annuli because the stratified sampling used to select specimens for intensive processing also selected all the large fish which would most likely show these marks.

Repeated examination suggests that age determination of *C. nothus* is consistent. We had 90% agreement in a second reading of scales from 225 fish, which included 123 fish >150 mm SL and all 38 fish first determined to have an annulus. The second reading identified an annulus in 45 specimens, including 30 of the 38 fish (79% agreement) first determined to have an annulus. The eight fish for which an annulus was not confirmed were collected in May and June about when the annulus forms; their scales had small marginal increments after an indefinite clear zone, and secondary radii and/or cutting over were not distinct. The second reading was done without knowing sizes or collection dates. This would minimize agreement between readings.

May-spawned *C. nothus* form an annulus from April (or earlier) to June when they reach 130-190 mm SL and 1 yr of age, but time of annulus formation may vary between spawned groups and is not clear for August- or September-spawned fish. Marginal increments were smallest from April to June and generally increased thereafter (Fig. 8), suggesting the first annulus forms from April (or earlier) to June. The smallest fish with an annulus was 139 mm SL and most exceeded 150 mm SL. The proportion with an annulus increased with increasing size, percentages being 16% at 150-159 mm SL ($n = 55$), 24% at 160-169 mm SL ($n = 54$), 60% at 170-179 mm SL ($n = 10$), and 100% at 180 mm SL and greater ($n = 6$). The proportion of the fish >150 mm SL with an annulus (Fig. 9) was significantly higher in May and June, when most of these large fish were May-spawned, than it was in September and November, when most were August- or September-spawned. Fish with an annulus in the period August-November all exceeded 170 mm SL and probably were survivors of the May_{76} group; those without an annulus then were 150-170 mm SL and probably August- or September-spawned.

Back-calculated lengths agree with length frequencies. Lengths at age I back-calculated using the Lee method (Lagler 1956) varied from 132 to 176 mm SL in comparison to 130-190 mm SL based on length frequencies. The mean back-calculated length was 156 mm SL with 95% confidence limits of 153-159 mm.

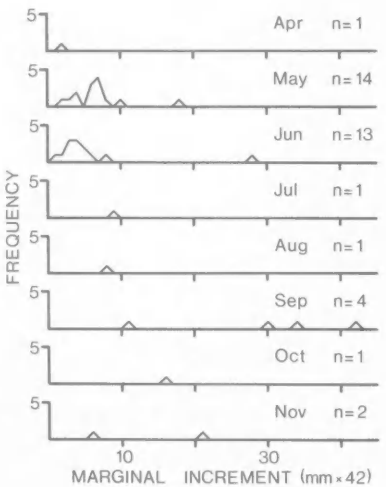

FIGURE 8.—Monthly marginal increments for *C. nothus* with one mark.

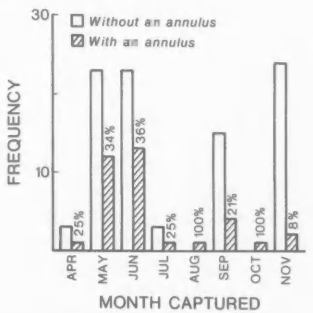

FIGURE 9.—Histogram showing by month the number and percentage of *C. nothus* >150 mm SL with and without an annulus.

Maximum Size, Life Span, and Mortality

Silver seatrout off Texas are small fish whose maximum life span (t_L) is about 1-1.5 yr. The largest of the 17,820 specimens that we captured were only 190 mm SL (230 mm TL). Almost 90% of the *C. nothus* captured off Port Aransas were <110 mm SL (Fig. 10), 99.1% were <160 mm SL, and 99.9% were <180 mm SL. Off Freeport, 85% were <110 mm SL, 99% were <160 mm SL, and 99.9% were <180 mm SL (Fig. 11). All *C. nothus* disappeared off Texas when they were slightly older than age I (Table 3).

The total annual mortality rate of *C. nothus* in the gulf off Texas approaches 100% and has a best estimate of 99.83%. Values of total annual mortality ($1 - S$) in each of the 9 mo from October 1977 through July 1978 off Freeport were 100% based on the expression $S = N_t/N_0$ where S = rate of survival and N_0 and N_t are the number of fish in consecutive year classes 0 and t. Only one year class was present off Freeport in those months so that $N_t = 0$. For the same reason, $1 - S$ was 100% off Port Aransas in each of the 4 mo from February through May 1977, during November and December 1977, and during March 1978. Mortality estimates were 98% and 99.9% for September and October off Port Aransas, assuming that fish >140 and >150 mm SL were from the older year class. For June, July, and August, $1 - S$ could not be estimated from the Port Aransas data, because the younger year class had just hatched and was incompletely recruited. However, if the predominant group in August had hatched in spring 1977, then $1 - S$ would approach 100% in that month also. Following the first procedure of Robson and Chapman (1961), we calculated an average value of $1 - S = 99.83\%$ by pooling the identifiable N_0 and N_t values for each month.

Distribution and Availability

Larger *C. nothus* seem more susceptible to trawling during the day. Few fish >100 mm SL were taken in night collections at 11, 18-24, and 29-31 m (Fig. 12), but many were taken in day collections at 7, 13-15, and 18-24 m.

Large silver seatrout almost disappeared during winter. Fish >120 mm SL from the May$_{77}$- and August-September$_{76}$ spawned groups were common during November off Port Aransas (Fig. 3) and during October and November off Freeport (Fig. 4), but very few were captured

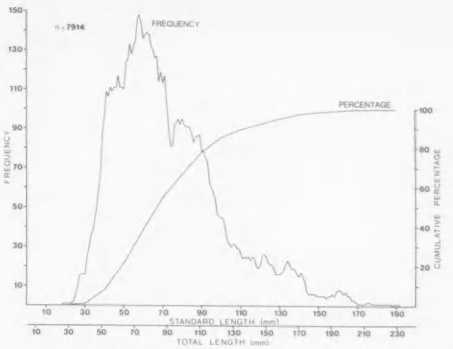

FIGURE 10.—Length frequency (moving averages of three) and cumulative percentage of all *C. nothus* collected off Port Aransas, Tex., February-December 1977.

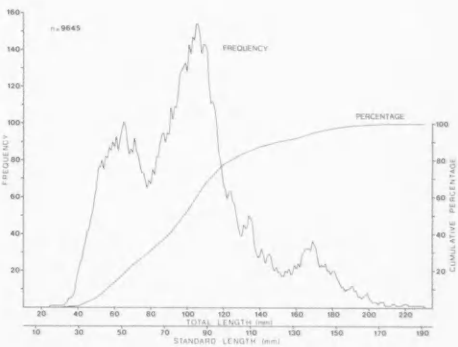

FIGURE 11.—Length frequency (moving averages of three) and cumulative percentage of all *C. nothus* collected off Freeport, Tex., October 1977-July 1978.

from December through March. The larger specimens of the August$_{77}$-spawned group also disappeared about December, which may be why the August- and September-spawned groups were not distinct thereafter. Many large fish were again taken in May or June.

Total Weight- and Girth-Standard Length and Standard Length-Total Length Relationships

Regression and related analyses for total weight-standard length, girth-standard length, and standard length-total length relationships are presented in Table 4. All regressions were

TABLE 4.—Analyses of total weight-standard length, girth-standard length, and standard length-total length relationships for *C. nothus*. Lengths and girths are in millimeters and weights are in grams.

Equation	n	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{x}$	$\bar{y}$
$\log_{10}$ TW = −4.7582 + 3.0077 $\log_{10}$ SL	2,451	0.0014	63.75	580.16	1.9056	0.9733
G = 6.64 + 0.63 SL	2,451	12.87	2,429,280	996,341	86.0	60.8
SL = −7.48 + 1.54 G	2,451	31.37	996,341	2,429,280	60.8	86.0
SL = −3.76 + 0.84 TL	303	7.48	587,667	420,074	101.5	81.8
TL = 4.98 + 1.18 SL	303	10.46	420,074	587,667	81.8	101.5

significant at $\alpha = 0.01$. Coefficients of determination (100 r^2) were 97% for girth-standard length relationships but 99% for total weight-standard length and standard length-total length relationships. All relationships were based on fish whose standard length range was 26-188 mm.

DISCUSSION

Spawning

Our findings on *C. nothus* reproduction agree with the limited literature. The finding of spawning from May to late October is consistent with reports of 1) fish about 35-40 mm TL (26-30 mm SL) or smaller from June to December (Hildebrand and Cable 1934; Hoese 1965; Christmas and Waller 1973; Mahood 1974), 2) ripe individuals in mid-May (Miller 1965) and throughout August (Gunter 1945; Hildebrand 1954), and 3) late-developing specimens in August and September (Mahood 1974). Our finding of peak spawning in late summer agrees with Gunter (1945) and Chittenden and McEachran (1976), and with the dominance of a late summer-spawned group in Mahood (1974, fig. 13). The small size at maturity is consistent with Miller's (1965) report of running ripe females only 135-140 mm TL (110-114 mm SL), although the smallest fish that Mahood (1974) collected in late-developing or spent condition was 205 mm TL (168 mm SL). Our finding of May-, August-, and September-spawned groups is similar to the spring peak and late summer or fall peak of reproduction reported for *C. nothus* (Mahood 1974) and for *C. arenarius* (Shlossman and Chittenden 1981). The latter workers suggested that the spawning periodicity of *C. arenarius* was timed to coincide with the two major periods of rising sea level in the northern Gulf of Mexico each year when surface currents could transport eggs and/or larvae to inshore or estuarine nurseries. Spawning of *C. nothus* in the Gulf of Mexico probably is timed also to take advantage of such current transport. We have observed that *C. nothus* exhibits two distinct peaks of spawning within the August-September major spawning period. It is not yet clear 1) whether multiple-spawned group production consistently occurs within the late summer reproduction period, which would imply spawning keyed to regular intraperiod cues, or 2) whether multiple-spawned group production in the late summer period reflects irregular happenstances such as the increased survival and recruitment that could occur if reproduction at times coincided with unusually favorable current transport (Hjort 1914, 1926; Nelson et al. 1977), or if a critical larval period (Marr 1956; May 1974) irregularly coincided with an unusually great food supply.

Growth and Age Determination

Our estimates that *C. nothus* in the northern Gulf of Mexico reach 130-190 mm SL and average 150 mm or more when they disappear at age I agree with Chittenden and McEachran (1976) and Chittenden (1977) that *C. nothus* reaches 120-150 mm SL (150-185 mm TL) at age I. Gunter's (1945) estimate that fish 75-110 mm SL (93-138 mm TL) taken in May were about 1 yr old is low and may have been based on fish that actually would not have reached age I until the major spawning period of August-September. None of these cited workers, though, recognized the multiple-spawned group composition of this species and their estimates of age could be in error. Our estimates for *C. nothus* agree with estimates for *C. nebulosus* of 157-165 mm SL at age I (Pearson 1929; Moody 1950; Tabb 1961), although lower estimates of 116 and 130 mm SL have been reported (Klima and Tabb 1959; Moffett 1961). The growth of *C. nothus* also agrees with estimates for *C. regalis* of 143-180 mm SL at age I (Merriner 1973). Seasonal growth of August-September spawned *C. nothus* appears comparable to that of *C. nebulosus* and *C. regalis*. Pearson (1929) found

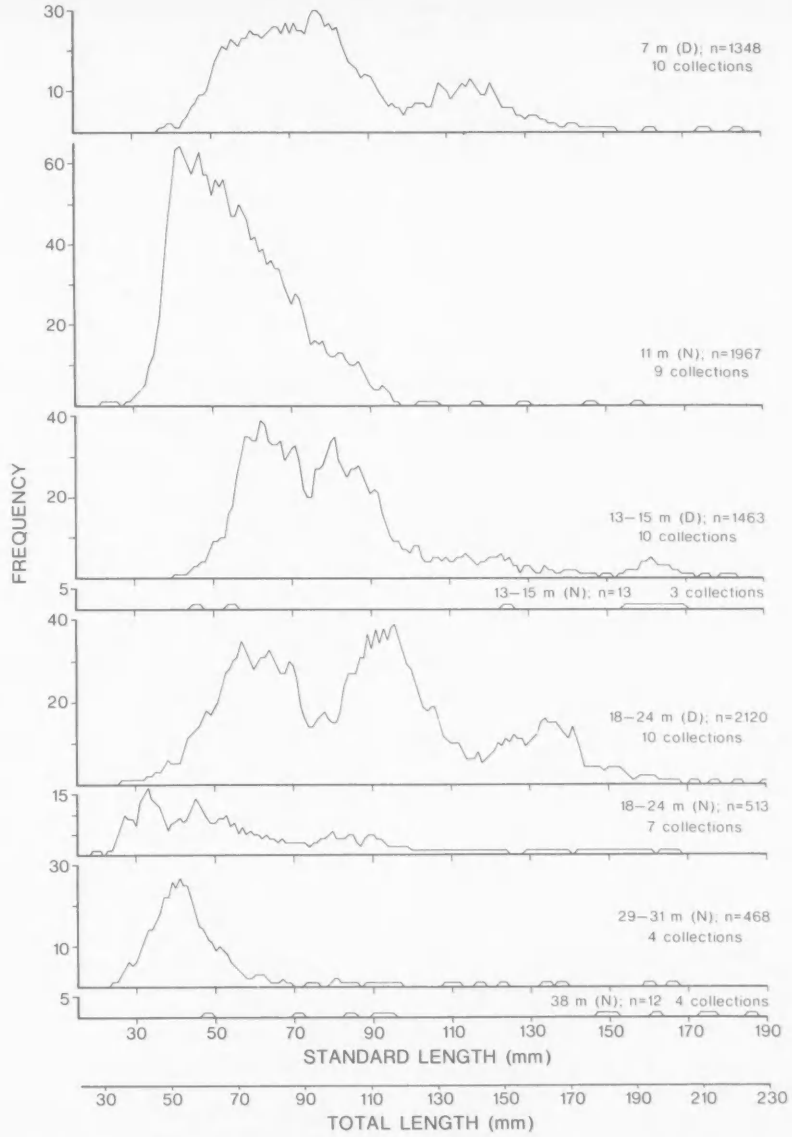

FIGURE 12.—Pooled length frequencies (moving averages of three) of *C. nothus* collected by day (D) and night (N) off Port Aransas, Tex., at each depth.

a similar seasonal growth pattern for *C. nebulosus* from Texas, but he did not calculate monthly increments. Estimates of monthly growth for *C. regalis* at age 0 are about 30-55 mm TL during the summer (24-45 mm SL) and about 10 mm TL in October (Welsh and Breder 1923; Hildebrand and Cable 1934; Pearson 1941).

Scales can be used to age *C. nothus*, but age de-

termination would probably be as accurate from intensive length frequencies alone. The long spawning season and multiple-spawned group compositions complicate age determination. Exact age determination may be difficult for the few fish age II or older. The few fish of these ages might not be distinct in length frequencies and a spawned group probably could not be assigned. Growth and mortality estimates for *C. nothus* should be based upon individual spawned groups to avoid misinterpretation.

Maximum Size, Life Span, and Mortality

The largest specimen of *C. nothus* that we captured (190 mm SL = 230 mm TL) is similar to the maximum sizes typically reported (Hildebrand and Cable 1934; Gunter 1945; Hildebrand 1954; Christmas and Waller 1973; Chittenden and McEachran 1976). The only published records of fish much >190 mm SL include a specimen 315 mm SL (380 mm TL) from the Gulf of Mexico off Mississippi (Franks et al. 1972), a few specimens to 259 mm SL (312 mm TL) from industrial fish catches in the gulf (Thompson 1966), and Mahood's (1974) report of two fish 255 mm SL (308 mm TL) from the Atlantic Ocean off Georgia. Net avoidance and/or behavioral change to a midwater life-style probably does not explain the absence of *C. nothus* >190 mm SL off Texas, because we collected many *C. arenarius* to 283 mm SL. Large *C. nothus* apparently do not occupy water deeper than 46 m off Texas, because twice monthly day and night collections at 55-100 m in the period June 1979-August 1980 have not captured larger fish (Chittenden, unpubl. data). The absence of large *C. nothus* off Texas might indicate movement to rough, normally untrawled substrate or possibly a spawning or postspawning movement to the northcentral gulf. Large *C. nothus* to 225-250 mm SL occur in deep water in the northcentral gulf (E. Gutherz and B. Rohr[6]), but the comparative percentage of these large fish needs further study. Based on our data and the published literature, however, it appears that *C. nothus* does not exist in significant numbers at sizes >190 mm SL. Even Mahood's (1974) data indicate that only 4% of his specimens were >188 mm SL.

[6]E. Gutherz and B. Rohr, Fishery Biologists, Southeast Fisheries Center Pascagoula Laboratory, National Marine Fisheries Service, NOAA, Pascagoula, MI 39567, pers. commun. January 1981.

The maximum life span of *C. nothus* is only 1-1.5 yr off Texas, although it might be as long as 2 yr in the northcentral gulf or off the southeast United States. A value of t_L = 1-1.5 yr seems reasonable for Texas waters because fish >160-180 mm SL (the average size at age I) made up <1-0.5% of our catch. Our estimate is supported by the absence of fish with more than one annulus and by the complete disappearance of fish after age I. This agrees with Chittenden and McEachran's (1976) estimate that the life span is little more than 1 yr. A t_L value as large as 2.0 yr seems tenable only for Mahood's (1974) data and, possibly, for the northcentral gulf where some fish reach larger sizes than we observed.

Our observed mortality estimates agree with theory (White and Chittenden 1977; Royce 1972: 238) that the total annual mortality rate is 90-100% if the life span is only about 1-2 yr. Our best estimate that $1 - S$ is 99% may be a slight overestimate, particularly if large fish exhibit significant spawning or postspawning migration to the northcentral gulf. However, it seems unlikely that many fish survive beyond 2 yr and that $1 - S$ is <90%. This is supported by Mahood's (1974) data which suggest a 96% mortality rate for *C. nothus* off the southeast coast of the United States, assuming that all his specimens >188 mm SL were age II fish. The high mortality rate that we have found explains why few *C. nothus* had an annulus. Most fish probably die before or while a mark forms on the scales.

Distribution and Availability

The disappearance of large *C. nothus* that we found during winter agrees with Mahood (1974, table 8), who reported only six specimens (of 947 fish) >130 mm SL (160 mm TL) from October through April, and with Hildebrand and Cable (1934), who reported no *C. nothus* captured off Beaufort Inlet, N.C., during winter although they were rather common in summer. The disappearance of large *C. nothus* during the colder months and their subsequent reappearance in spring probably reflects an offshore overwintering movement of large fish. This interpretation is supported by 1) reanalysis of Chittenden and McEachran's (1976, fig. 10) data on distribution of *C. nothus* in mid-January (Fig. 5) which indicates that fish >140 mm SL were most abundant in deep water, and 2) Miller's (1965) report that large *C. nothus* occurred in deep water from February through April.

General

The production of several spawned groups over a broad time period in each annual spawning season is extremely important to the population dynamics of *C. nothus*. This species is short-lived and appears little more than an annual crop whose abundance could fluctuate greatly from year to year. However, the multiple-spawned group structure would buffer against population instability just as a multiple year class structure buffers population size in longer lived species. The multiple-spawned group feature may average over a longer period each year the effects of environmental variation on spawning success, may dampen fluctuations in annual spawning success associated with environmental extremes, and may stabilize population sizes. Similarly, the effects of fishing would be averaged over a greater number of spawned groups in 1 yr, so that the multiple-spawned group structure might minimize the possibility of recruitment overfishing. In that event, stock assessments based on dynamic pool models and growth overfishing would be more valid.

Many features of the population dynamics of *C. nothus*—short life span, high mortality rate, and rapid turnover of biomass—are similar to those in the Atlantic croaker, *Micropogonias undulatus*, of the Carolinean Province (White and Chittenden 1977; Chittenden 1977). This supports the suggestion (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the gulf have evolved towards a common pattern of population dynamics. Because of their similar population dynamics, the implications of Chittenden's (1977) simulations on croaker could serve as a first approximation of the effects of harvesting *C. nothus*, so that this species also should have a great biological capacity to resist growth overfishing.

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CYCLOGRAPSUS INTEGER H. MILNE EDWARDS, 1837 (BRACHYURA, GRAPSIDAE): THE COMPLETE LARVAL DEVELOPMENT IN THE LABORATORY, WITH NOTES ON LARVAE OF THE GENUS *CYCLOGRAPSUS*

ROBERT H. GORE AND LIBERTA E. SCOTTO[1]

ABSTRACT

The complete larval development of *Cyclograpsus integer*, a small sesarmine grapsid crab, is described and illustrated from larvae reared in the laboratory. *Cyclograpsus integer* attains five, and often six, zoeal stages plus one megalopal stage. Temperature affects both duration of larval development and number of larval stages. At 25°C, the megalopal stage was attained in 26-27 days from fifth stage zoeae and 31-32 days from sixth stage zoeae, while metamorphosis at 20°C occurred in 53-55 days from sixth stage zoeae. The zoeal and megalopal stages of *C. integer* are compared to all known cultured species of the genus and morphological differences are noted. *Cyclograpsus integer* zoeae may be distinguished from both other species in the genus and other species in the family by its antennal morphology, being the only species with the type A antenna (i.e., the exopodite about equal in length to the protopodite). Megalopae of this species may be distinguished from other species in the genus by the formation of the frontal region and the terminal setation of the telson. Other potentially useful zoeal morphological characters are discussed regarding both the taxonomic and phylogenetic position of *C. integer*.

The sesarmine genus *Cyclograpsus* is cosmopolitan, containing at least 16 species, 13 of which occur in the Indo-West Pacific region (Griffin 1968). *Cyclograpsus integer*, one of four species in the genus occurring in the New World and the only one known from the western Atlantic, is quite widespread with records from western and eastern Africa, and localities in the Indo-West, eastern central, and northern west Pacific Ocean (Monod 1956; Griffin 1968; Manning and Holthuis 1981). Although Rathbun (1918) listed the Peruvian and South American species *Cyclograpsus cinereus* Dana, 1851 as being the eastern Pacific analog to *C. integer*, Griffin (1968) noted that *Cyclograpsus escondidensis* Rathbun, 1933, an eastern Pacific species known only from Central America, was closer to *C. integer* than to any other member of the genus. In the same study, Griffin described *Cyclograpsus sanctaecrucis*, a new species from Santa Cruz Island in the southwestern Pacific Ocean, stating that "Except in the presence of a lateral notch on the carapace, [this] species most closely resembles *C. integer*." Thus, *Cyclograpsus integer* appears similar to at least two other species in the genus from the Pacific Ocean.

The larvae of members of the genus are not well known, and the complete larval development has been determined for only two New World species at present. Costlow and Fagetti (1967) described and illustrated the complete development of *C. cinereus* from Chile, and in a subsequent paper Fagetti and Campodonico (1971) recorded the development of a species from Juan Fernandez Islands which they identified as *Cyclograpsus punctatus* H. Milne Edwards, 1837. Griffin, however (1968), suggested that specimens of *Cyclograpsus* from those islands are actually referable to *Cyclograpsus lavauxi* H. Milne Edwards, 1837, stating that *C. punctatus* is restricted to South Africa. To add to this confusion, Wear (1970) described and illustrated the first zoeal stages of two New Zealand species, *Cyclograpsus insularum* Campbell and Griffin, 1966, and *C. lavauxi*. But a comparison of his illustrations of the latter species with the first zoeal stage figured by Fagetti and Campodonico shows substantial differences in the number and position of chromatophores, appendage processes, and segmentation of the maxillule, suggesting that notable variation occurs between eastern and western Pacific populations of *C.*

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lavauxi, if Fagetti and Campodonico's species was misidentified. These differences raise the possibility that the New Zealand (Wear 1970) and Chilean (Fagetti and Campodonico 1971) forms of *C. lavauxi* are subspecies, assuming that Griffin is correct in restricting *C. punctatus* to South Africa. On the other hand, the Chilean specimens may indeed have been correctly identified as *C. punctatus*, thus accounting for the observed differences in the larvae, as well as reinstating the Juan Fernandez Islands as the westernmost zoogeographical boundary for the species. Until further data are available, we will consider Fagetti and Campodonico's species to be correctly identified as *C. punctatus*, so that we may compare the morphological features of this species with others in the genus.

The aforementioned confusion, and the widespread occurrence of *C. integer*, as well as its close morphological relationship to *C. escondidensis*, its Central American analog, all illustrate the importance of determining the larval development of these species. Accomplishing this would facilitate identification of their respective larvae in the plankton and also allow comparisons of morphological features in zoeal and megalopal stages. The latter stages provide a means of elucidating phylogenetic relationships both intra- and intergenerically among the Grapsidae. Accordingly, in this paper we describe and illustrate the complete larval development of *Cyclograpsus integer* and compare salient characters shared by the zoeae and megalopae in *C. punctatus*, *C. cinereus* from the New World, and *C. lavauxi* and *C. insularum* first zoeae from the Indo-West Pacific.

MATERIALS AND METHODS

Three ovigerous females (carapace width 7.0, 9.3, 10.4 mm) were collected among medium-sized cobbles in the high intertidal zone at Bodden Town, Grand Cayman Island, on 15 July 1980. Following previous methodology (Gore 1968), the crabs were maintained in 19 cm diameter glass bowls filled with seawater (34‰) and fed *Artemia* spp. nauplii daily until hatching occurred on 25, 28, and 29 July 1980 (largest to smallest female, respectively). A total of 192 larvae were cultured in eight 24-compartmented polystyrene trays, one larva per compartment. The eight trays were maintained in controlled temperature units in a diel fluorescent light cycle of 12 h light, 12 h dark. A total of 144 larvae (72 at each temperature) were cultured at 20° and 25°C (±0.5°C). Another 48 larvae were maintained at 15°C (±0.5°C). Seawater (34-36‰) was changed and the larvae were fed *Artemia* nauplii daily. All dead larvae, molts, and representative live specimens were preserved in 70% ethanol. Descriptions and illustrations were made with the aid of dissecting stereomicroscope and compound microscope with camera lucida attachments, using specimens from all three hatches. Measurements are the arithmetic mean of all specimens examined in a given stage. Carapace length was measured from the base of the rostrum to the posterior margin of the carapace, lateral view in zoeae and dorsal view in megalopae. Carapace width in the latter was measured dorsally across the widest part of the carapace. In all descriptions, setal formulae progress distally.

The first 4 zoeal stages are denoted as ZI to ZIV. One series of fifth zoeal stages (ZVu; ultimate) molted directly to megalopa stage; another (ZVp; penultimate) molted to a sixth (ZVI) stage. The morphological differences in these two forms are noted in the text.

A complete larval series and/or their molts is deposited in the National Museum of Natural History, Washington, D.C. (USNM 184669); the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 2328-1); the British Museum (Natural History), London (1981-447); the Rijksmuseum van Natuurlijke Historie, Leiden (D-34220); the Museum National d'Histoire Naturelle, Paris (M.N.H.N.-B7294, 7295); and the Indian River Coastal Zone Museum, Fort Pierce, Fla. (IRCZM 89:5096). The adult females are divided among the National Museum of Natural History, the Indian River Coastal Zone Museum, and the Paris Museum.

RESULTS OF THE REARING EXPERIMENT

Temperature not only influences the duration of larval development within stages, but also affects the number of zoeal stages attained (Table 1, Fig. 1). At the warmer temperature (25°C) either 5, or occasionally 6, zoeal stages occurred. However, the single first crab stage was reached after 37 d in the laboratory by a megalopa which molted from a stage V zoea. Of 3 other stage V zoeae that molted to stage VI, only 2 eventually reached megalopa and none sur-

TABLE 1.—Duration in days of larval and postlarval stages in *Cyclograpsus integer* at two laboratory-culture temperatures. (Mean based only on larvae attaining next stage.)

Temperature (°C)	Stage	Minimum	Mean	Mode	Maximum	Number molting to next stage (or dying in molt)
25	Zoea I	5	6.6	6	11	44
	II	4	4.3	4	6	22 (+2)
	III	4	4.2	4	6	18
	IV	4	4.2	4	5	14
	Zoea V-Megalopa	4	5.2	6	6	5 (+2)
	Zoea V-VI	4	4.0	4	4	3
	Zoea VI-Megalopa	6	6.0	6	6	2
	Megalopa (V)	11	—	—	—	1
	Megalopa (VI)	All died in stage after 1 day				0
20	Zoea I	9	10.9	10 (13)[1]	14 (21)[1]	21 (+1)
	II	7	9.2	8	17	14
	III	6	7.3	8	9	13
	IV	7	7.9	8	9	10
	Zoea V-Megalopa	No fifth stage zoeae molted to megalopa				
	Zoea V-VI	6	7.7	7-8	12	9
	Zoea VI-Megalopa	11	11.7	12	12	6 (+1)
	Megalopa	18	21.7	—	25	3

[1]Died in stage.

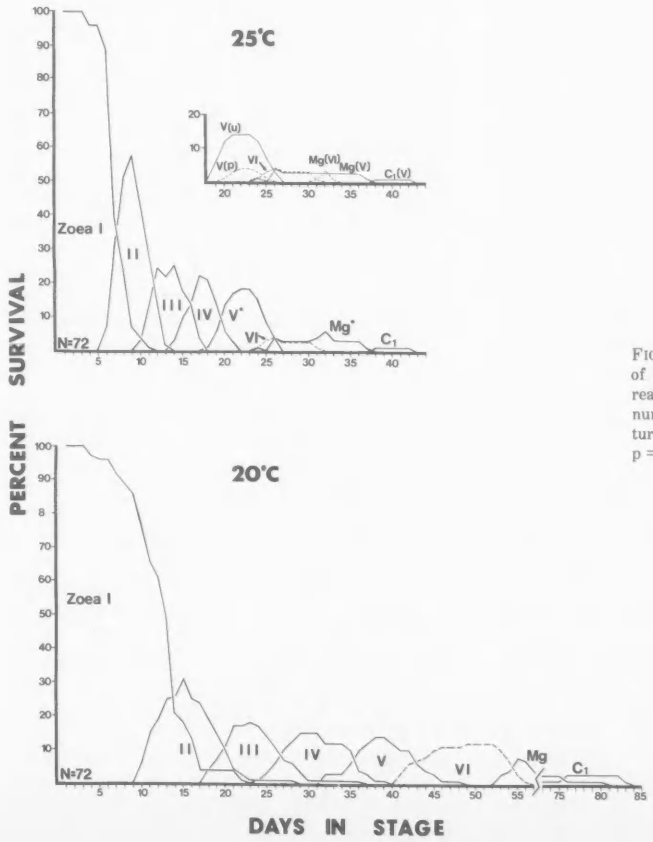

FIGURE 1.—Percent survival and duration of larval stages in *Cyclograpsus integer* reared under laboratory conditions. N = number of larvae cultured at each temperature; * = combined stages; u = ultimate stage; p = penultimate stage. [See text.]

vived to first crab stage. The time period of 37 d may well be a reasonable reflection of what takes place in the plankton, because at 25°C in the laboratory a hypothetical zoea passing through the minimum duration for each stage could conceivably attain first crab stage in as few as 32 d (5 stages) or 38 d (6 stages) after hatching.

The variation in duration of each zoeal stage at 25°C (except for the first zoea) was rather low, comprising no more than 2 d. Stage I, however, could last from 5 to 11 d, although most individuals molted to stage II between 6 and 7 d after hatching. A single zoea that remained in stage I for 11 d also molted to stage II, but died the following day. A comparison of the values in Table 1 with the survival graph (Fig. 1) shows that mortality was quite high on the days just prior to, and during, the ecdysial period in stage I, but as development progressed the mortality subsequently fell. These results are similar to others obtained in our laboratory with brachyuran and anomuran larvae, and indicate that the more mature zoeal stages have a greater survival potential. This might be a result of one or a combination of factors, including the type, quality, and amount of food consumed, the genetic makeup of the parents, or a response by the larvae to unfavorable physical conditions in the laboratory (see Bookhout and Costlow 1970; Knowlton 1974; Gore et al. 1981, for summaries of the various hypotheses).

At 20°C, both within-stage and overall developmental duration were more variable. Extended zoeal durations and the production of a sixth zoeal stage were both noted at the cooler temperature. Larvae remained in stage I 9-14 d before proceeding with further development. Most larvae molting to stage II did so 10 d after hatching. However, a larger component of zoeae died than survived during this ecdysis, most dying at day 14, with 3 zoeae lasting until day 21. It would seem that whatever general effect the lower temperature has on zoeal stages cannot be overridden after about 12-13 d in the first stage, so that the larvae eventually die if they have not molted by this time. Once stage II was reached, most zoeae were capable of continuing their development with relatively little mortality compared to that seen in stage I (Fig. 1). Modal values of within-stage developmental time were generally twice that seen at 25°C. The rearing data also show that the megalopal stage was attained following 6, rather than 5, zoeal stages, approximately 53-55 d after eclosion. Another 18-25 d were required before the first crab stage was reached. Thus, a minimum of 73 d was required after hatching to complete development, even though an extrapolation from the minima in Table 1 suggests that a hypothetical zoea might possibly reach first crab stage in as few as 64 d after hatching at 20°C. Extended developmental times such as these are not necessarily detrimental if the larvae can avoid predation and find sufficient and suitable food. Such longer periods of development could aid in the dispersal of the larvae, thereby accounting, at least in part, for the wide distribution of the adults of this species. However, at the lower temperature of 15°C, all of the 48 larvae remained in stage I up to 12 d before dying. This high mortality suggests very unfavorable conditions for the survival of this species.

Cyclograpsus integer, along with some species of *Sesarma*, is among the few Sesarminae, and among still fewer Varuninae and Plagusiinae (Wilson 1980; Wilson and Gore 1980) known to have extra larval stages. The species presently stands alone in the genus in having this feature, but joins an increasingly large group of brachyuran (and anomuran) crustaceans in which an additional larval stage occurs either at lower, or perhaps suboptimum, temperatures (Sandifer 1973; Knowlton 1974; Scotto 1979; Gore et al. 1981). The studies just cited follow classic investigations by Costlow et al. (1960), Bookhout (1972), and Bookhout and Costlow (1974) in which temperature and salinity were manipulated and the effects on survival, duration, and number of larval stages were observed. The data in all these studies add to a large body of circumstantial evidence from the plankton (e.g., alleged substages, morphological variants, oversized larvae, etc.) which suggests that additional larval stages may be an integral part of a decapod crustacean's larval potentiality in nature, and not just an artifact observed during laboratory culture of the species. Whether extra stages occur commonly, or only rarely, they are still classifiable as a response to change in conditions, and as such constitute an evolutionary adaptation toward survival.

Description of the Larvae

First Zoea

Carapace length: 0.38 mm; 5 specimens examined.

Carapace (Fig. 2A, a).—Smooth, globose, dorsal spine short, slightly curving posteriorly, rostral spine stout, bluntly rounded, ventrally directed; no lateral spines present in this stage. A mediodorsal knob (Fig. 2a) midway between bases of dorsal and rostral spines with 5 integumental sensilla arranged as illustrated, these present in all stages. Posterolateral margin of carapace indistinctly and irregularly dentate; ventrolateral margin produced into a blunt V-shaped process. Paired setae posterolaterally to base of dorsal spine in all stages. Eyes unstalked.

Abdomen and Telson (Fig. 2B).—Five somites; first naked, second, third, and fourth with paired lateral knobs (fourth smallest) directed anteriorly, ventrally, and laterally respectively, these also with bluntly rounded posterolateral process; fifth somite with bluntly rounded posterolateral process. Pair of posterodorsal setae on somites 2-5 in all stages. Telson rectangular with pair of short, minutely hairy, furcae, 6 spines in between, each armed with rows of spinules. Shallow median notch present.

Antennule (Fig. 2C).—Conical rod directed anteriorly, flanking rostral spine, with 4 aesthetascs of varying size.

Antenna (Fig. 2D).—Biramous; protopodite and exopodite spinelike processes approximately equal in length, both armed with 2 rows of spinules; exopodite with a simple seta one-third distance from base.

Mandibles (Fig. 2E).—Asymmetrically scoop-shaped process; incisor process with 1 large tooth anteriorly as well as posteriorly, 3 bluntly rounded denticles in between, plus 3 similarly on posterior edge of right mandible, 2 on left; molar process irregularly dentate, a large rounded tooth on the posterior angle.

Maxillule (Fig. 2F).—Endopodite 2-segmented, setal formula progressing distally 1,5 (4 terminal plus 1 subterminal); basal endite with 5 stout setae, coxal endite with 4 stout, 1 thinner seta. Additional pubescence as illustrated.

Maxilla (Fig. 2G).—Endopodite irregularly bilobed, each with 2 setae; basal and coxal endite bilobed, setal formula proximally to distally 5,4 and 4,3, respectively. Scaphognathite with 4 plumose setae on outer margin, distal portion tapering to setose apical process. Other pubescence as illustrated.

Maxilliped 1 (Fig. 2H).—Coxopodite naked; basipodite with 9 ventral setae, progressing distally 2,2,3,2; endopodite 5-segmented, setal formula 2,2,1,2,4+I (Roman numeral = dorsal setae), third segment with several minute hairs on dorsal surface; exopodite indistinctly 2-segmented, 4 terminal natatory setae.

Maxilliped 2 (Fig. 2I).—Coxopodite naked; basipodite with 4 ventral setae, progressing distally 1,1,1,1; endopodite 3-segmented, setal formula 0,1,5+I; exopodite indistinctly 2-segmented, 4 natatory setae.

Color.—Overall golden-brown under refracted light, abdomen colored more intensely than cephalothorax. Cornea black under refracted, iridescent blue under reflected light. Grouped brown and orange chromatophores appear as follows: carapace, 4 interocular, 1 at base of dorsal spine, 1 at position of posterodorsal knob, 2 at future position of lateral spines, 4 along posterior margin, 3 at posteroventral angle; appendages, 1 on mandibles, 1 each on antennular and antennal protopodites, 2 on each maxillipedal basipodite; abdomen, 1 pair ventromedially on first somite, second through fifth somites with 1 pair anteroventrally and 1 pair posteroventrally; telson with 1 pair anteriorly and 1 pair posteriorly at base of each set of 3 spines.

Second Zoea

Carapace length: 0.50 mm; 5 specimens examined.

Carapace (Fig. 3A).—Enlarged, pair of ventrally curved lateral spines now present. Dorsal and rostral spines both elongated, thinner, ends more tapered than first stage. Pair of interocular and 1 posterolateral seta now present. Posterodorsal knob midway between base of dorsal spine and posterior edge of carapace more prominent. Eyes stalked.

Abdomen and Telson (Fig. 3B).—Similar in shape and armature to first stage with addition of single long dorsal seta on posteromedial edge of first somite.

Antennule (Fig. 3C).—As in first stage but with 6 unequal aesthetascs.

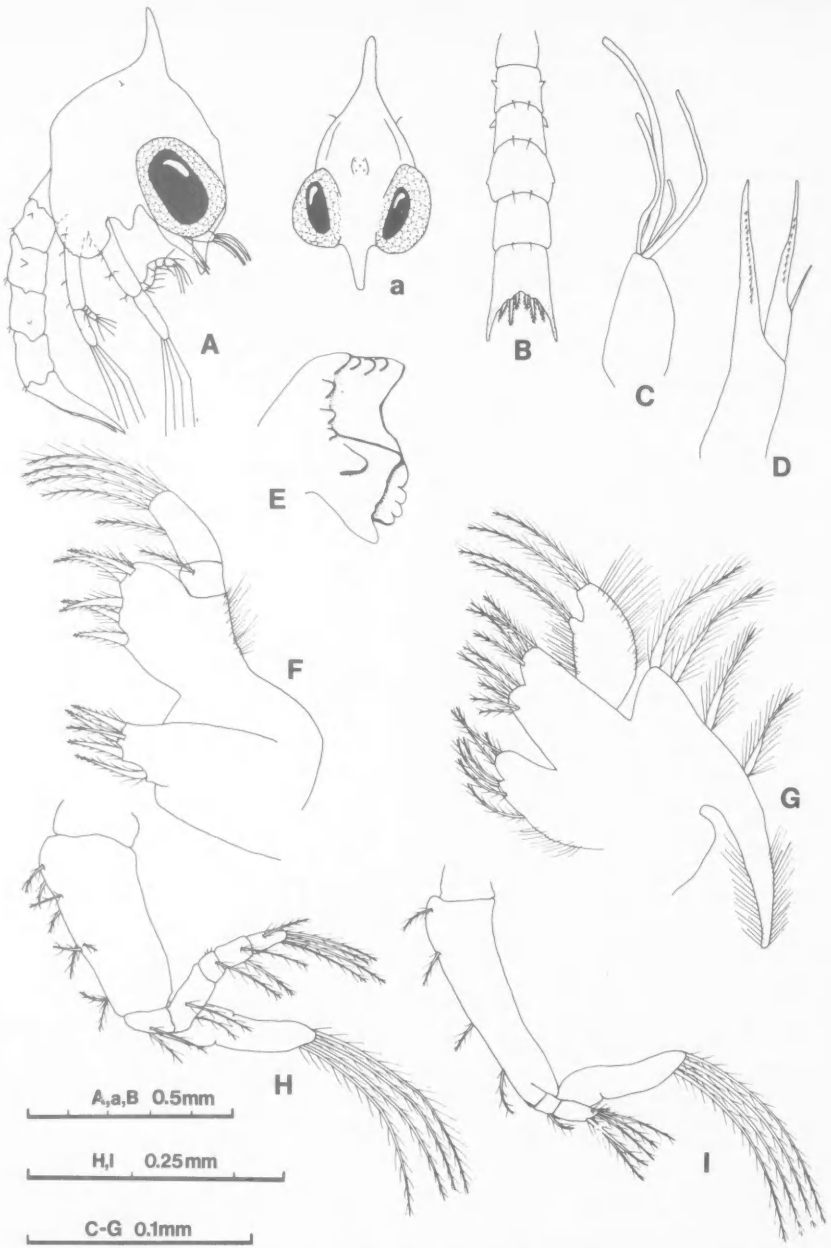

FIGURE 2.—First zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (a) anterodorsal view; (B) abdomen and telson (in dorsal view as illustrated here and throughout all stages); (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

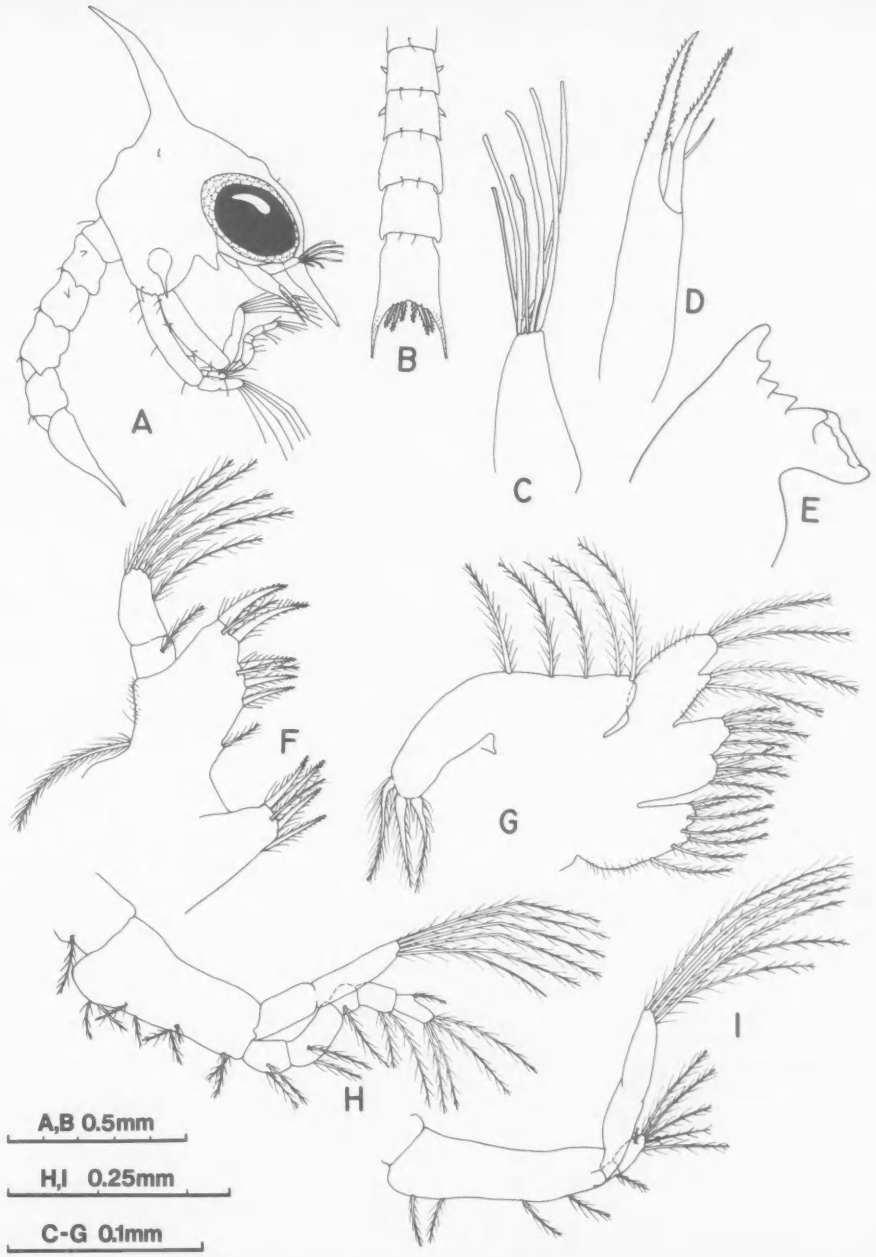

FIGURE 3.—Second zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

Antenna (Fig. 3D).—Similar in form and armature to first stage, with addition of minute hair on exopodite opposite of simple seta one-third from base.

Mandible (Fig. 3E).—Increased in size, shape and armature similar to first stage.

Maxillule (Fig. 3F).—Endopodite and coxal endite setation unchanged. Basal endite now with 5 stout, 3 thinner setae plus 1 long plumose seta on basal margin.

Maxilla (Fig. 3G).—Endopodite, basal, and coxal endite setation unchanged. Scaphognathite with 5 long, thin, plumose setae proximally, 3 stout plumose setae on distal margin.

Maxilliped 1 (Fig. 3H).—Coxopodite with 1 ventral seta. Basi- and endopodite setation unchanged. Exopodite with 6 natatory setae.

Maxilliped 2 (Fig. 3I).—Coxo-, basi-, and endopodite setation unchanged. Exopodite now with 6 natatory setae.

Color.—Overall darker golden brown than first stage. Color much more intense at dorsal spine, fifth somite, and telson. Lateral spines, rostrum, maxillipedal endo- and exopodites transparent. Deep golden hue around base of dorsal spine. Other chromatophore color and position as in first stage.

Third Zoea

Carapace length: 0.70 mm; 5 specimens examined.

Carapace (Fig. 4A).—Zoea much enlarged, dorsal, rostral, and lateral spines elongate, 2 pair of interocular setae, posterodorsal knob more prominent, posterolateral margin now with 4 or 5 setae placed as illustrated, irregular denticulation ventral to setae present here and in all stages. Posterodorsal margin of carapace with 3 setae.

Abdomen and Telson (Fig. 4B).—Sixth abdominal somite now present, with small bluntly rounded posterolateral process. First somite with 3 dorsomedial setae, middle the longest. Paired lateral knobs on second and third somites enlarged, posterolateral processes on somites 2-5. Telson with interfurcal setal formula now 4+4, innermost pair the shortest.

Antennule (Fig. 4C).—Unchanged in form from second stage, with 4 unequal aesthetascs.

Antenna (Fig. 4D).—Similar to second stage, exopodite now slightly shorter than protopodite.

Mandible (Fig. 4E).—Similar in form and armature to second stage.

Maxillule (Fig. 4F).—Endopodite and basal endite armature unchanged, 1,5 and 8+1 processes basally, respectively. Coxal endite with 5 setae plus 1 long plumose seta on basal margin.

Maxilla (Fig. 4G).—Endopodite 2,2, as before, basal endites 5,4, coxal endites now 5,3. Scaphognathite setae increased to 10 thinner plus 6 stout distal setae, separated by sparse hairs as illustrated.

Maxilliped 1 (Fig. 4H).—Coxo- and basipodite setation unchanged. Endopodite setal formula now 2,2,1 plus spine replacing dorsal setae, 2, 4+I. Exopodal natatory setae 8.

Maxilliped 2 (Fig. 4I).—Coxo-, basi-, and endopodite setation unchanged. Exopodite with 8 natatory setae.

Color.—Now appearing ocherous orange. Dorsal spine, abdomen, and telson darkest. Lateral spine with orange coloration on ventral surface. Orange chromatophores: at base of rostral spine, another midway to tip; on 2 or 3 basipodite of maxillipeds. Sixth somite and telson each with pair of orange-brown chromatophores medioventrally. Other chromatophore pattern remains as in first stage.

Fourth Zoea

Carapace length: 0.80 mm; 5 specimens examined.

Carapace (Fig. 5A).—Similar in form to third stage, elongate dorsal spine now with 5 setae on anterior margin as illustrated. Posterodorsal border now with 4 setae, posterolateral margin with 6. V-shaped process on ventrolateral margin less blunt than previous stages.

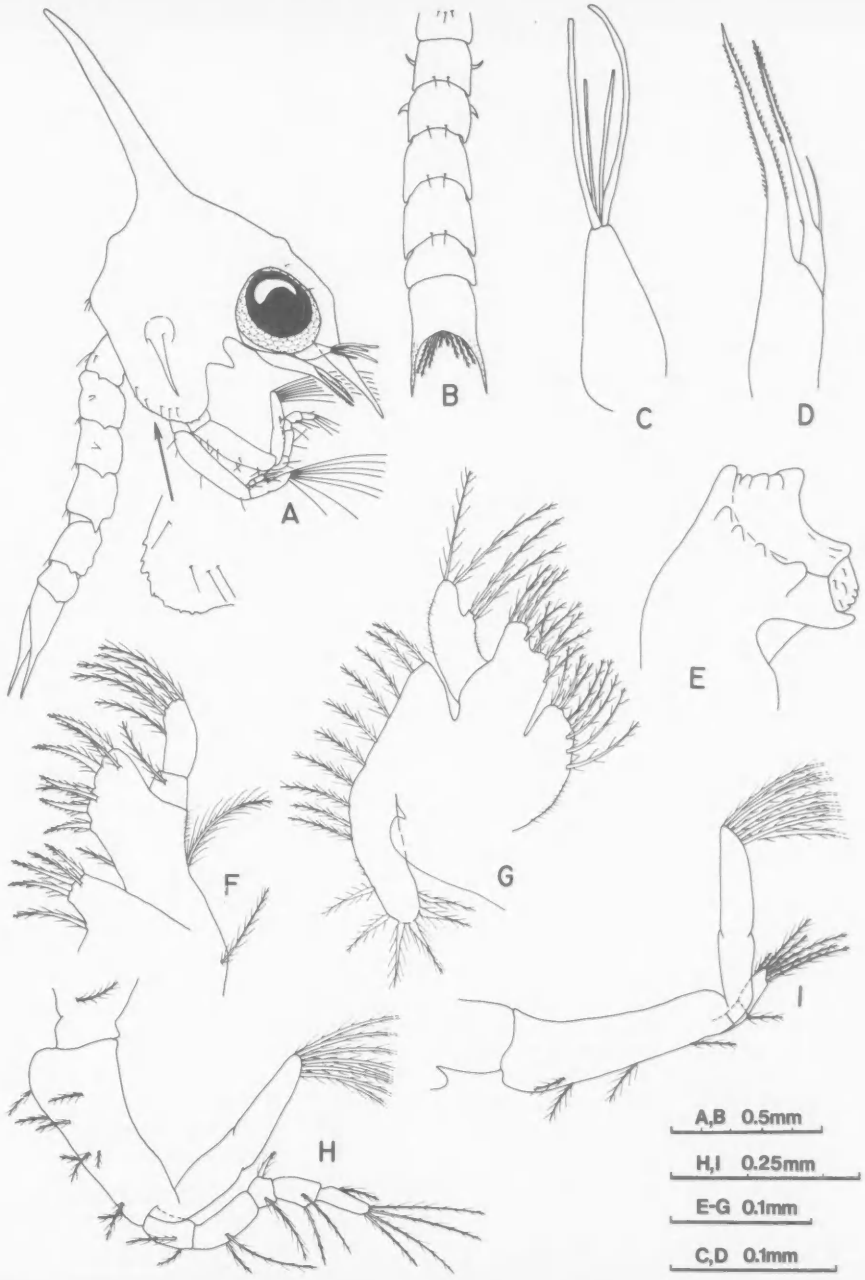

FIGURE 4.—Third zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

FIGURE 5.—Fourth zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandibles; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

Abdomen and Telson (Fig. 5B).—Pleopod and uropod buds now present on somites 2-5 and 6, respectively. First somite now with 5 middorsal setae.

Antennule (Fig. 5C).—Conical rod with 5 terminal plus 2 subterminal aesthetascs.

Antenna (Fig. 5D).—Armature and form similar to previous stage. Endopodal bud now present, less than one-half length of protopodal process.

Mandible (Fig. 5E).—Similar to third stage with addition of 1 bluntly rounded tooth on posterior edge of incisor process.

Maxillule (Fig. 5F).—Endopodite setation unchanged, basal endite now with 11 or 12 setae, coxal endite with 8 setae, 3-5 plumose setae on basal margin, placed as illustrated.

Maxilla (Fig. 5G).—Setal formulae on endopodite 2,2; basal endites 6,5; coxal endites 7,3. Scaphognathite with 17-21 thinner setae, plus 5 or 6 stouter distal setae.

Maxilliped 1 (Fig. 5H).—Coxopodite now with 2 ventral setae. Basipodite setation unchanged. Endopodite now with 2,2,1 plus 1 spine, 2,5+I. Exopodal natatory setae 9.

Maxilliped 2 (Fig. 5I).—Coxo-, basi-, and endopodal setation unchanged. Exopodite now with 9 natatory setae.

Color.—Ocherous orange; additional orange and brown chromatophores appear together as follows: 1 each posterior to eyestalks, 1 anteromedially on somites 2-4, a pair anteroventrally on somites 5 and 6, 1 anteroventral plus another medioventral pair on telson, and 1 each at base of lateral spine.

Fifth Zoea (Ultimate)

Carapace length: 1.2 mm; 3 specimens examined.

Carapace (Fig. 6A).—Similar to previous stage, dorsal spine elongate, posterodorsal border with 4 setae, posterolateral margin with 8 setae.

Abdomen and Telson (Fig. 6B).—First somite with 6 or 7 middorsal setae, all other morphological features similar to fourth stage. Pleopod buds elongate, all now with endopodites.

Antennule (Fig. 6E).—Endopodal bud present laterally below 2 tiers of aesthetascs, 5 unequal terminal aesthetascs plus 1 seta, and 6 subterminal aesthetascs. Basal region swollen, unsegmented.

Antenna (Fig. 6F).—Endopodal bud now three-fourths length of protopodal process. Exopodal spine remains shorter than protopodite.

Mandible (Fig. 6I).—Palp bud present on anterior surface. Incisor and molar form and armature as in fourth stage.

Maxillule (Fig. 6J).—Endopodal setation unchanged. Basal endite with 15 or 16 setae, coxal endite with 10-13 setae, 3 additionally on basal margin.

Maxilla (Fig. 6K).—Endopodite unchanged. Setae of basal endites 8,8, coxal endites 11,4. Scaphognathite with 31-33 marginal setae.

Maxilliped 1 (Fig. 6L).—Coxopodite now with 3 ventral setae. Basi- and endopodite setation unchanged. Exopodite now with 11 natatory setae.

Maxilliped 2 (Fig. 6M).—Coxo-, basi-, and endopodal setation unchanged. Exopodite now with 12 natatory setae.

Maxilliped 3 (Fig. 6N).—Rudimentary trilobed, unsegmented naked process.

Color.—Similar to previous stage. Numerous additional brown and orange chromatophores appear especially on anterior region of cephalothorax and sixth abdominal somite and telson. Tips of maxillipedal exopodites now with orange hue. On day before metamorphosis to megalopa, ultimate fifth stage zoea has very dark brown cephalothorax with innumerable spidery brown and orange chromatophores interspersed. Dorsal spine and abdomen vermilion. Coalesced orange and brown chromatophore occur posteriorly on the eyestalk.

Fifth Zoea (Penultimate)

Carapace length: 1.1 mm; 3 specimens examined.

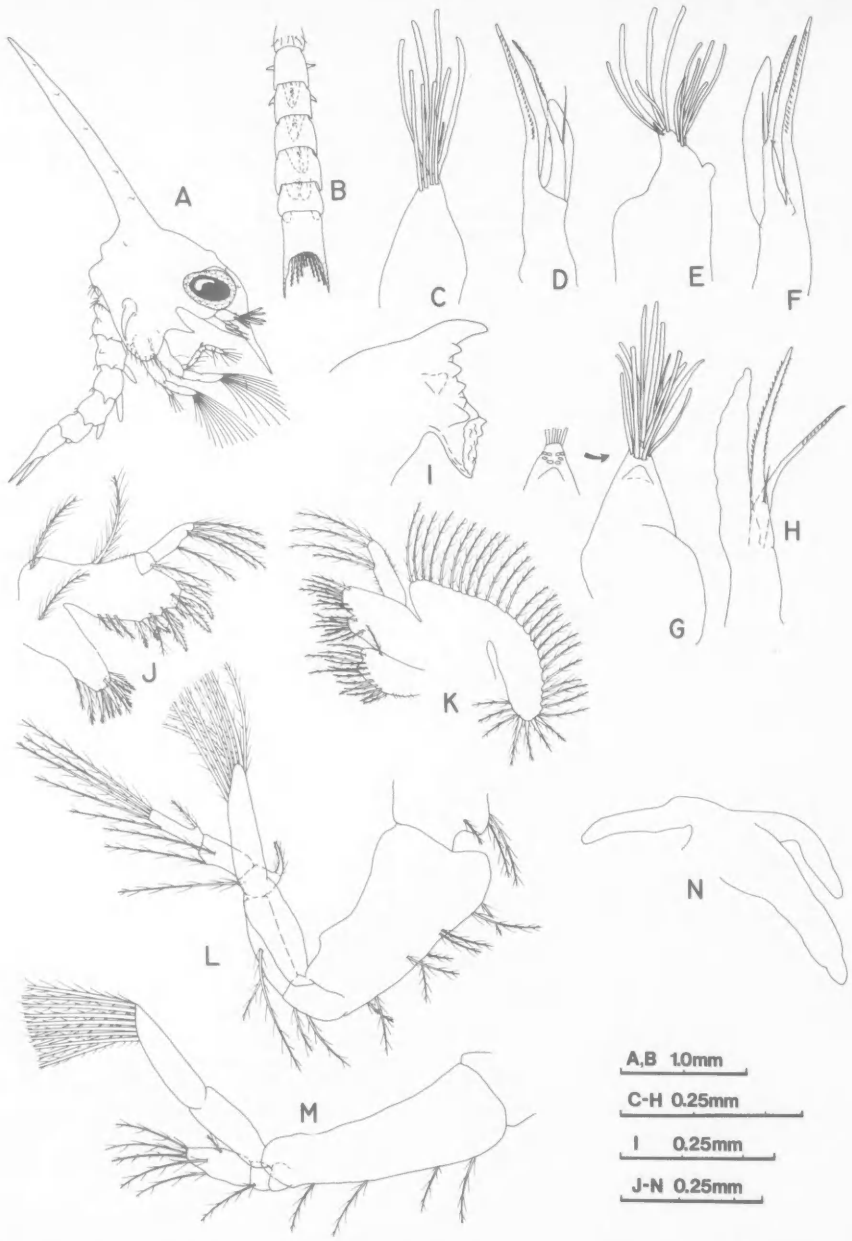

FIGURE 6.—Fifth (ultimate, A, B, E, F, I-M, penultimate, C, D) and sixth (G, H) zoeal stages of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C, E, G) antennule; (D, F, H) antenna; (I) mandible; (J) maxillule; (K) maxilla; (L) maxilliped 1; (M) maxilliped 2; (N) maxilliped 3.

Remarks.—The penultimate fifth stage zoea molted to a sixth stage before metamorphosing to megalopa. Only morphological features differing significantly from the ultimate fifth stage, which molts directly to megalopa, are discussed below.

Antennule (Fig. 6C).—No endopodal bud present, 5 terminal plus 4 subterminal unequal aesthetascs present.

Antenna (Fig. 6D).—Endopodal bud only one-half length of protopodal process, other armature and processes similar.

Mandible.—No palp present, other armature similar.

Abdomen.—Pleopod buds without endopodites, less elongate and developed.

Sixth Zoea

Carapace length: 1.3 mm; 3 specimens examined.

Remarks.—The sixth stage zoea appear similar in form and armature to the ultimate fifth stage. Only morphological characters which may be used to distinguish between the two stages are discussed below.

Carapace.—Little inflated, posterodorsal border with 6 setae.

Abdomen and Telson.—First somite with 8 or 9 middorsal setae, pleopod buds more elongate.

Antennule (Fig. 6G).—Aesthetascs arranged in tiers as illustrated, progressing distally 2,2,4,4.

Antenna (Fig. 6H).—Endopodal bud obscurely segmented, five-sixth length of protopodal process.

Mandible.—Palp more elongate.

Maxillule.—Basal endite with 18 setae, coxal endite with 12 setae, basal margin with 3 or 4 plumose setae.

Maxilla.—Basal endites with 9,8, coxal with 12,4 setal formulae. Scaphognathite with 34-37 marginal setae.

Maxilliped 1.—Coxopodite with 4 or 5 ventral setae. Basipodite setal formulae variable from 9 to 11 ventral setae, exopodite with 12 or 13 natatory setae.

Maxilliped 2.—Coxopodite naked or with 1 seta ventrally, endopodite setation variable either 0,1,5+I or 1,1,5+I. Exopodite with 13 or 14 natatory setae.

Maxilliped 3.—Trilobed as in fifth stage, may have 1 seta on each lobe.

Color.—Similar to fifth stage, innumerable spidery brown and orange chromatophores, entire maxillipeds now orange brown.

Megalopa

Carapace length × width: 1.45 × 1.25 mm; 7 specimens examined.

Remarks.—Megalopae molting from both fifth and sixth zoeal stages are similar in form and armature. Morphological characters distinguishing megalopae, which molted from ZVI, are placed in brackets under the appropriate headings.

Carapace (Fig. 7A, B).—Cephalothorax subquadrate, laterally inflated. Smooth surface covered with hairs as illustrated, plus innumerable setae on posterior and posterolateral borders. Frontal region developed into ventrally deflexed, bluntly rounded rostrum with distinct median cleft, appearing as U-shaped sinus viewed dorsally. Anterolateral margins of carapace produced into 2 indistinctly rounded lobes. Eyes large, projecting laterally.

Abdomen and Telson (Fig. 7A, a, E-I).—Somites 1-5 with bluntly rounded posterolateral processes, somite 6 much broader than long; all with setae as illustrated; telson semicircular, no posterior marginal setae, 2 pairs medially, others as illustrated. Pleopods well developed, with variable setation 16-19, 20 or 21, 19-22, 22 [19-21, 21, 22, 22], all endopods with 3 hooked setae terminally. Uropods with 10 or 11 exopodal plus 1 protopodal seta [11 or 12 plus 1].

Pereopods (Fig. 7A, C, D).—Chelipeds well developed, somewhat inflated, unarmed, equal, shorter than walking legs, gape of chelae irregularly serrated, setae on remaining articles as

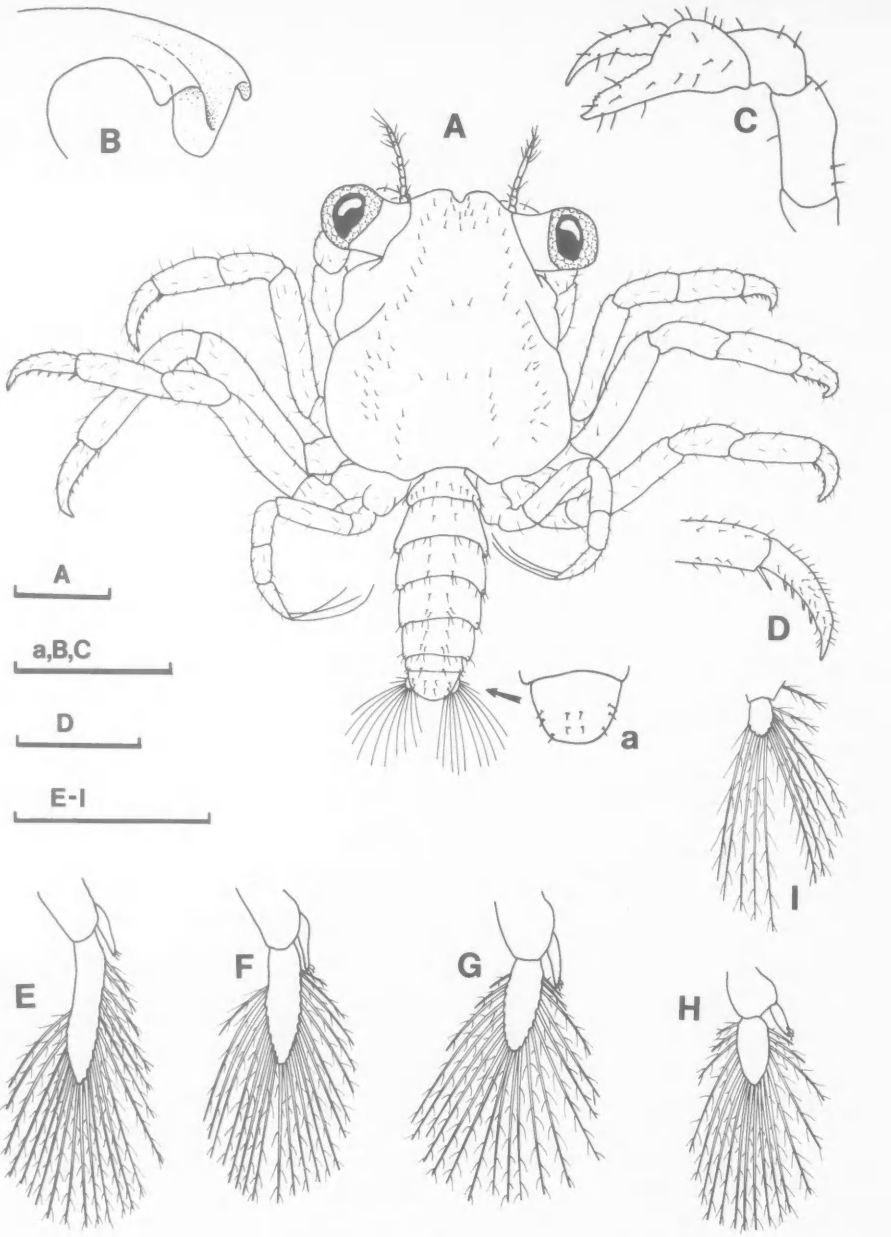

FIGURE 7.—Megalopa stage of *Cyclograpsus integer*. (A) Dorsal view; (a) telson; (B) rostrum (anterolateral view); (C) left cheliped; (D) second pereopod dactyl; (E) first pleopod; (F) second pleopod; (G) third pleopod; (H) fourth pleopod; (I) uropod. Scale lines = 0.5 mm.

illustrated. Second to fourth pereopods elongate, similar, each with distoventral tooth on propodus and 4 ventral teeth on dactyl. Fifth pereopod dactyl with 3 [3 or 4] long pectinate setae (= brachyuran feelers).

Antennule (Fig. 8A).—Biramous, peduncle 3-segmented, extremely enlarged, bulbous basal segment with 2 or 3 [3-5] setae, middle segment much smaller ovoid, with 2 or 3 [3 or 4] setae, distal segment larger than middle, expanded distally, naked. Flagellar lower ramus 1-segmented, 3 terminal, 1 subterminal setae; upper ramus 4-segmented, tiered aesthetascs usually arranged (0)(6), (6, plus 1 lateral seta), (5, plus 1 terminal seta).

Antenna (Fig. 8B).—Peduncle with 2-4 distal setae; flagella with setation 1,2,0,0,2-3, 0,5,3,3, [1,2,0,0,4,0,4-5,3,3-4].

Mandible (Fig. 8C).—Incisor process smooth, spatulate; molar process elongate, tubular; palp 2-segmented with 0,9 setae.

Maxillule (Fig. 8D).—Endopodite irregularly shaped, with 4 distal, 2 or 3 lateral setae; basal endite with 12 spines, 12-14 setae [25-29], coxal endite with 8 spines plus 2 rows of about 9 or 10 processes each [32] arranged in tiers as illustrated. Basal margin with 4 [3-5] long setae.

Maxilla (Fig. 8E).—Endopodite unsegmented, 2 [3] setae on lower lateral margin. Basal endites with 9-11, 12-14, [10-12, 13-16] processes, coxal endites with 7, 18-20 [8 or 9, 20-22] processes. Scaphognathite with 61-62 marginal setae plus 5 laterally on the blade as shown [70-72 plus 5].

Maxilliped 1 (Fig. 8F).—Exopodite 2-segmented, with 2 distal, 4 terminal setae. Endopodite irregularly shaped, unsegmented, 4-8 setae scattered over length. Basal endite with 13-17 [15-17], coxal endite with 17-20, setae. Epipodite with 9 or 10 [13-18] long, aesthetascoid processes.

Maxilliped 2 (Fig. 8G).—Exopodite 2-segmented, 2 lateral, 4 terminal setae. Endopodite 5-segmented setation progressing distally 3-7, 1, 1, 3 or 4, 6 or 7. Epipodite with 4-7 distal, 1 proximal, aesthetascoid processes, [9-11, plus 1]. Protopodite setae not determined.

Maxilliped 3 (Fig. 8H).—Exopodite 2-segmented with 5 or 6 proximal, 4 or 5 terminal setae; endopodite 5-segmented setae progressing distally 16-18, 12 or 13, 8-10, 10 or 11, 6 or 7 [18-20, 13, 8-12, 9-12, 8], protopodite with 21 or 22 [22-26] setae, epipodite with 21-26 aesthetascoid processes distally plus 8 or 9 setae proximally [30-32, plus 8-11].

Color.—Innumerable spidery orange and brown chromatophores completely covering cephalothorax, abdomen, pereopods, eyestalks, and all feeding appendages.

DISCUSSION

Zoeal Stages

The complete larval development of <20% of the known species of *Cyclograpsus* has been studied, and zoeal stages within the genus will be difficult to identify in the plankton. Larvae of the genus are unusual in several respects; therefore, some morphological and developmental characters may yet prove to be of aid in identification. For example, in at least two species (*C. integer* and *C. cinereus*) lateral carapace spines are lacking in the first stage, but appear in all later stages (Costlow and Fagetti 1967). Within the genus, some form of armature occurs on the ventrolateral carapace margin, either as spines, small teeth, setae, or a combination of these. In general, teeth or spines occur in the early stages and are replaced by setae as development proceeds. The number and time of appearance of these processes seems to be species specific (Table 2; and summary in Fagetti and Campodonico 1971). In addition to the ventrolateral processes, later larval stages of all species of *Cyclograpsus* studied to date bear some form of setation of spination on the posterior middorsal margin of the carapace above the insertion of the abdomen. In *C. cinereus*, this takes the form of paired spines in the second and subsequent zoeal stages (Costlow and Fagetti 1967); in *C. punctatus*, a similar situation appears in the third and later stages (Fagetti and Campodonico 1971), whereas in *C. integer*, 3 setae appear in the third and subsequent stages.

Unfortunately, the characters noted above are not restricted to *Cyclograpsus* but are shared, at least in part, among zoeae of several other genera in the four grapsid subfamilies. For instance, several genera in the Grapsinae, Varuninae, and Sesarminae have zoeal stages which lack lateral

FIGURE 8.—Megalopa stage of *Cyclograpsus integer*. (A) Antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3.

TABLE 2.—Comparison of selected zoeal characters in five species of *Cyclograpsus*.

Species	Carapace spines: Dorsal	Carapace spines: Lateral	Ventro-lateral	Appendages antennule	Antennae (exopod)	Maxilliped 1: Basipod	Maxilliped 1: Endopod	Maxilliped 2: Basipod	Maxilliped 2: Endopod	Abdomen/(telson) armature
C. cinereus (Costlow and Fagetti 1967)										
Zoea I	Gibbose	Absent	5 spines	2 aesth., 2 setae	Protopod 1.3× exopod (1 lat. spine)	[1]1,2,3,3	2,1,1,2,4+I	1,1,1,1	0,1,1+3+I	Somite 2 spined; (I+3)
Zoea II	Curved	Present	6 spines, 6 setae	4 aesth.	Protopod 1.5× exopod	[1]1,2,3,3	2,2,1,2,4+I	1,1,1,1	0,1,1+3+I	Somite 2 spined; (I+3)
Zoea III	Curved	Present	5 spines, 10 setae	4 aesth.	Protopod 1.5× exopod	[1]2,1,3,3	2,2,1+I,2,4+I	1,1,1,1	[1]0,1,2+3+I	Somite 2 spined; (I+4)
Zoea IV	Nearly straight	Present	4 spines, 14 setae	5+1 aesth.	Protopod 1.6× exopod (1.4× endopod)	[1]1,1,3,3	2,2,2,2,1+4+I	1,1,1,1	[1]0,1,2+3+I	Somite 1 with 5 dorsal spines
Zoea V	Straight	Present	10 spinules, 18 setae	5+4 aesth., 2 lateral setae	Protopod 1.8× exopod (0.7× endopod)	[1]4,2,3,2?	2,1+II,1+I, 1+I,1+4+I	1,1,1,1	0,1,1+3+II	Somite 1 with 5 dorsal spines
C. punctatus (Fagetti and Campodonico 1971)										
Zoea I	Curved	Present	12 spines	2 aesth., 2 setae	Protopod 1.25× exopod (2 lat. spines)	2,2,3,3	2,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 spined; (I+3)
Zoea II	Nearly straight	Present	2 setae	4 aesth.	Protopod 1.5× exopod	2,2,3,3	2,2,1,2,4+I	1,1,1,1	0,2,2+3+I	Somites 2,3 spined; (I+3)
Zoea III	Nearly straight	Present	11 setae	5 aesth.	Protopod 1.4× exopod	2,2,3,3	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somite 1 with 3 setae; (I+4)
Zoea IV	Nearly straight	Present	12 setae	6+1 aesth.	Protopod 1.1× exopod (2.9× endopod)	2,2,3,3	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somite 1 with 3 setae; (I+4)
Zoea V	Nearly straight	Present	15 setae	4+4 aesth., 1 lateral	Protopod 1.23× exopod (1.4× endopod)	2,2,3,4	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somite 1 with 3 setae; (I+5)
C. integer										
Zoea I	Slightly curved	Absent	Irregularly dentate	4 aesth.	Protopod ≅ exopod (1 lat. seta)	2,2,3,2	2,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2-4 with knobs (I+3)
Zoea II	Slightly curved	Present	1 seta	6 aesth.	Protopod ≅ exopod (1 lat. seta)	2,2,3,2	2,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs
Zoea III	Nearly straight	Present	5 setae	4 aesth.	Protopod ≲ exopod	2,2,3,2	2,2,1+I,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea IV	Sparsely setose	Present	6 setae	5+2 aesth.	Protopod 1.2× exopod (1.9× endopod)	2,2,3,2	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea V (U)	Sparsely setose	Present	8 setae	5+6 aesth., 1 lateral seta	Protopod 1.07× exopod (1.18× endopod)	2,2,3,2	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea V (P)	Sparsely setose	Present	8 setae	5+6 aesth.	Protopod 1.05× exopod (1.75× endopod)	2,2,3,2	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea VI	Sparsely setose	Present	8 setae	2,2,4,4 aesth.	Protopod 1.18× exopod (= endopod)	9-11 setae (variable)	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I or 1,1,2+3+I	Somites 2,3 with knobs (I+4)
C. lavauxi (Wear 1970)										
Zoea I	Slightly sigmoid	Present	ca. 7 setae	3 aesth.	Protopod 1.3× exopod (3 lat. setae)	[1]2+1,1,1,1	1,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+3)
C. insularum (Wear 1970)										
Zoea I	Slightly curved	Present	ca. 20 small teeth	4 aesth.	Protopod 1.5× exopod (3 lat. setae)	3,3,3,3	2,2,1,2,4+I	1,1,1,1	0,2,2+3+I	Somites 2-4 spined; (I+3)

[1]Data interpolated from illustrations.

carapace spines. No first stage grapsine zoeae, no *Sesarma* (Sesarminae), nor *Acmaeopleura* (or possible *Gaetice*) larvae in the Varuninae have these spines (see summary in Wilson 1980). Moreover, *Pachygrapsus* zoeae (Grapsinae), like some larvae in *Cyclograpsus*, apparently lack lateral spines in the first, but possess these in subsequent, zoeal stages (Schlotterbeck 1976; Bourdillon-Casanova 1960). On the other hand, all known plagusiine larvae have lateral spines from the first stage onward (Wilson 1980).

Setation or spination on the ventrolateral carapace margin is another widely shared feature among grapsid genera. Examples include *Brachynotus* (Bourdillon-Casanova 1960), *Hemigrapsus* (Kurata 1968), and *Cyrtograpsus* (Scelzo and Lichtschein de Bastida 1979) in the Varuninae, *Sesarma* (Baba and Miyata 1971) in the Sesarminae, *Leptograpsus* (Wear 1970) in the Grapsinae, and *Plagusia* (Wilson and Gore 1980) in the Plagusiinae. In many instances, however, carapace and telson spine formulae differ substantially from that seen in larvae of *Cyclograpsus*, thereby allowing at least provisional separation among these zoeae.

Regarding middorsal carapace setation, many descriptions of brachyuran larvae either fail to note its occurrence or do not allow judgment to be made because of undetailed illustrations. A general perusal of the literature available on grapsid larvae (Wilson 1980) shows that, in addition to *Cyclograpsus*, only a few sesarmine genera had this feature indicated, including *Chasmagnathus* (Boschi et al. 1967), *Helice* (Baba and Moriyama 1972), and in the Varuninae *Hemigrapsus* (Hart 1935) and *Cyrtograpsus* (Scelzo and Lichtschein de Bastida 1979). Several other studies provide suitably detailed illustrations which suggest that this character may be more or less widespread among the zoeae of these subfamilies. However, these setae are apparently absent in plagusiine and grapsine larvae, as far as can be ascertained from the literature. Because these setae usually do not appear until later zoeal stages (ZIII and beyond) their usefulness as an identifying character is somewhat limited.

One other carapace feature that seems noteworthy, at least for the genus *Cyclograpsus*, is the pterygostomian region of *C. integer*; this region is produced into a triangular, toothlike prominence in the first stage, which becomes more sharply pronounced as development proceeds. In *C. cinereus*, this prominence is always bluntly rounded until the last stage, when it becomes more acute. In *C. punctatus* the prominence develops very slowly and apparently never becomes acute. Only the first zoeal stages are known in *C. lavauxi* and *C. insularum* (Wear 1970) and the prominence is not well developed in either, being similar to that seen in *C. punctatus*. Although the toothlike prominence is seen to some extent in other grapsid zoeae, it does not appear to be quite as prominent, based on the illustrations provided in several studies.

The type of antenna has always been considered an important classification feature in brachyuran larvae (Aikawa 1929). Most brachyuran larvae have a type B antenna (i.e., exopod about 0.5-0.75× the length of the protopodal spine). This type is widely present throughout the Grapsidae, being found predominantly in the Sesarminae and Varuninae, but seen in only isolated instances in either the Grapsinae or Plagusiinae. Nearly all Grapsinae have a type C antenna (exopod substantially reduced in size to the protopodal spine), an advanced character also shared for the most part among the known larvae of plagusiine genera (see summary in Wilson 1980).

All *Cyclograpsus* larvae possess a type B antenna, with the exception of *C. integer*, which has a type A antenna (exopod and protopod about equal). The type A antenna is considered to be primitive (Aikawa 1929). The larvae of *C. integer* are even more remarkable in having the antennal protopodal spine and exopod both armed along their respective lengths with rows of teeth, in a manner similar to that seen in *Eriocheir* zoeae (Varuninae; Aikawa 1929), and reminiscent of some antennae exhibited by larvae in several xanthid genera (e.g., Scotto 1979). In other *Cyclograpsus* zoeae, the exopod is entire, and only the protopodal spine is so armed. *Cyclograpsus integer* is thus noteworthy for two exceptions: 1) an antenna of a form (i.e., doubly armed) rarely noted within the Grapsidae, and 2) an antenna type (A) found in no other zoeae of any genus in the Grapsidae.

Rice (1980) summarized the available knowledge on the Grapsidae in a major paper dealing with brachyuran zoeal classification. In attempting to delineate useful features among the four subfamilies of grapsid crabs, he suggested that the known zoeae of the Varuninae and Sesarminae might be distinguished from the Grapsinae and Plagusiinae by always having a well-developed antennal exopod at least half as long as the

spinous (protopodal) process (i.e., type B) and bearing at least 10 medial setae on the basis of the first maxilliped. Wilson (1980) subsequently demonstrated that *Euchirograpsus* larvae (Varuninae) have extremely shortened antennal exopods (type C) plus only 8 basipodal setae, and therefore are more allied to Grapsinae and Plagusiinae larvae than to those of the Sesarminae or other Varuninae. As noted above, *C. integer* also refute Rice's suggestion in regard to the Sesarminae, by having a type A antenna and by bearing 9 (instead of 10) basipodal setae. Larvae of *C. cinereus* also have 9 basipodal setae on maxilliped 1, but these occur in a grouping different from that seen in *C. integer*; *C. lavauxi* larvae have 6 and *C. insularum* have 12 setae (Table 2).

As to other features for distinguishing among the larvae of *Cyclograpsus*, setation and armature of abdominal somites can be useful. Beginning with the second (*C. integer*), third (*C. cinereus*), or fourth zoeal stage (*C. punctatus*), nonpaired, usually elongate or spinelike setae are found on the posterodorsal margin of the first abdominal somite. As development proceeds these setae either increase in number (1, 3, 5, in *C. integer* stages), or remain unchanged (3, *C. punctatus*; 5, *C. cinereus*). Somite armature shows similar diversity, with a hooklike spine or knob on the second (*C. cinereus*), second and third (*C. punctatus*, *C. lavauxi*), or second through fourth somites (*C. integer*, *C. insularum* first zoea). Regrettably, neither of these characters are specific for *Cyclograpsus* larvae because they occur in other brachyuran zoeae and are seen, for example, in the Goneplacidae (*Carcinoplax*, Lee and Hong 1970; *Tritodynamia*, Boucquet 1965), as well as several other families less closely related to the Grapsidae (Lebour 1928, fig. 5, p. 483).

The telsons in *Cyclograpsus* zoeae all seem referrable to Aikawa's (1929) type B (i.e., without supernumerary lateral spines, and typically brachyuran in shape). The telson formula of I+3 (= furcal spine, plus movable spiny seta; Gore 1979) changes in stage III to I+4 in *C. integer*, *C. cinereus*, and *C. punctatus*; the latter species, however, adds an additional medial pair of setae in stage V, becoming I+5. Table 2 provides a summary of all of these features.

Megalopal Stage

The megalopae of the three *Cyclograpsus* species in which complete development is known differ substantially from one another and should prove more easily separable than their respective larvae. The frontal region bears a strongly deflexed rostral spine in *C. punctatus* (Fagetti and Campodonico 1971), has a ventrally deflexed, bluntly rounded rostrum with a median cleft in *C. integer*, and is only slightly produced and without a rostral spine in *C. cinereus* (Costlow and Fagetti 1967). Other easily observed characters not requiring dissection include terminal setation on the telson, aesthetascs on the antennule, exopodal setae of the third maxillipeds, pleopods, and uropods. These, plus characters requiring some dissection to observe, are summarized in Table 3.

None of the megalopal stages in any of the three species considered resembles the juvenile or adult crabs. Moreover, they do not exhibit easily noticeable differences from many other brachyuran megalopae, let alone grapsid megalopae. In general, lack of rostral spines, or with the rostrum only poorly developed, usually deflexed, and unarmed, is seen in many grapsid postlarvae. Many of the species have the lower ramus of the antennule appearing as a 1-segmented, simple, palplike process (as in *Chasmagnathus*, *Helice*, *Cyrtograpsus*, and others, Costlow and Fagetti 1967), or even reduced to a simple seta (*Sesarma*; Costlow and Bookhout 1962). But because of the paucity of descriptions there is little use in attempting further classification at this time.

In the discussion above we have demonstrated that several suggestions proposed by Rice (1980) for classifying grapsid larvae can no longer be considered useful. Although the distinctions among the larvae of the subfamilies Grapsinae and Varuninae, and Varuninae and Sesarminae have become blurred, we nonetheless reiterate the value of Rice's classification attempt, and draw special attention to his key to the brachyuran families based on zoeal characters. By using the characters he proposed, one may still arrive within the Grapsidae using the key, provided that the subfamilial headings are disregarded. Rice's couplet 26 may then be modified to read as follows:

26. Carapace without lateral spines in *all zoeal stages* 27
    Carapace *usually* with lateral spines *in all zoeal stages or without only* in first zoeal stage 28

TABLE 3.—Comparison of selected megalopal characters in three species of *Cyclograpsus*.

	C. integer	*C. cinereus*	*C. punctatus*
Cephalothorax	Numerous hairs dorsally	Dorsally naked[1]	Dorsally naked[1]
Front	Bluntly rounded, ventrally deflexed medially cleft rostrum	Slightly produced, without rostral spine	Strongly deflexed rostral spine
Telson processes	0 terminal, 3 lateral, 2 pairs dorsally	3 terminal, 3 lateral, 2 pairs dorsally	9 terminal, 8 dorsal (6 transversely)
Antennular aesthetascs	(0)(6)(6,+1 seta) (5,+1 seta)	(0)(3)(4,+1 seta)(5)	(0)(4)(4,+2 setae) (4,+3 setae)
Antennal flagella	9 articles	11 articles	9 articles
Mandibular palp	0,9 setae	0,9 setae	0,7 setae
Maxillule			
Basipod	24-26 processes [25-29]	21 processes	ca. 24 processes
Coxopod	28-30 processes [32]	11 processes	16 processes
Basal margin	4 setae [3-5]	No data	2 setae
Maxilla			
Endopod	0, +2 lateral setae	2, +1 lateral setae	1, 1+4 lateral setae
Scaphognathite	61-62 marginal setae [70-72]	ca. 70 marginal setae	ca. 65 marginal setae
Maxilliped 3			
Exopod	5-6 proximal, 4-5 distal setae	3 proximal, 5 distal setae[1]	2 proximal, 5 distal setae[1]
Pleopods			
Exopod setae	16-22 [19-22]	17-20	15-16
Uropod setae	1 protopodal, 10-11 exopodal [11-12]	1 protopodal, 10 exopodal	1 protopodal, 8 exopodal

[1]Data interpolated from illustrations; no specific description given [ ] = megalopal stage obtained from zoeal stage VI.

We look to future studies that will provide descriptions of several common genera in the Grapsinae (e.g., *Geograpsus*, *Goniopsis*), Sesarminae (*Metapograpsus*), as well as to additional studies on larvae of previously known genera in the Plagusiinae (*Plagusia*, *Percnon*), and Varuninae (*Euchirograpsus*, *Cyrtograpsus*, and the as yet unknown zoeae of *Glyptograpsus*). All have the potential for providing further clarification of relationships among the Grapsidae.

ACKNOWLEDGMENTS

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REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE LONGSPINE PORGY, *STENOTOMUS CAPRINUS*[1, 2]

PAUL GEOGHEGAN[3] AND MARK E. CHITTENDEN, JR.[4]

ABSTRACT

Stenotomus caprinus mature at 90-125 mm TL as they approach age I. Spawning occurs once a year in a discrete period of 50-80 days duration from January through April with peak activity in February or March. The male-female sex ratio was 1:1.21 in the spawning period. Spawning occurs in waters deeper than 27 m, and its timing coincides with the periodicity of onshore surface currents in the northern Gulf of Mexico. These currents probably transport eggs and larvae inshore to nursery areas <27 m deep where recruitment occurs. Young-of-the-year gradually disperse as they mature to waters 36-55 m deep where age I and II fish are most abundant. *Stenotomus caprinus* are most vulnerable to trawling at night. Growth in length is fastest in their first 8 months but slows greatly as they mature and divert energy towards reproduction. *Stenotomus caprinus* averaged 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. Maximum size is about 200 mm TL and maximum lifespan typically is 2.5-3 years. Total annual mortality rate is 83-99%, but postspawning survival, mortality rates, and lifespan vary greatly between year classes. Total weight-total length, length-length, and girth-total length relationships are presented. The population dynamics of *S. caprinus* appear quite different from those of *S. chrysops*, and the genus *Stenotomus* may show zoogeographic change at Cape Hatteras, N.C.

Stenotomus caprinus, the longspine porgy, ranges in the Gulf of Mexico (Gulf) from Campeche Bank, Mexico, to Apalachee Bay, Fla., (Caldwell 1955) and occurs rarely in the Atlantic to North Carolina (Dawson[5]). It is very abundant at depths of 40-110 m and is the dominant fish in the brown shrimp community (Hildebrand 1954; Chittenden and McEachran 1976; Chittenden and Moore 1977). *Stenotomus caprinus* makes up a significant portion of the catch in the industrial fishery of the north central Gulf (Roithmayr 1965; Gutherz et al. 1975).

Despite its abundance, little is known about this species. Its life history is known from general faunal studies such as Miller (1965), Moore et al. (1970), and Franks et al. (1972), although Henwood et al. (1978) described its food habits. Only Caldwell (1955), Henwood (1975), Henwood et al. (1978), and Dawson (footnote 5) have made studies specifically directed at *S. caprinus*.

This paper describes maturation and spawning seasonality, movements and spawning areas, growth and sizes at age, mortality and lifespan, merits of age determination by scales and length-frequency analysis, length-length, total weight-total length, and girth-total length relationships for *S. caprinus*.

METHODS AND MATERIALS

Stenotomus caprinus were collected monthly along a transect in the Gulf off Freeport, Tex., (Fig. 1) from October 1977 through March 1980 aboard a chartered shrimp trawler using double rigged 10.4 m shrimp trawls with 4.4 cm stretched cod end mesh and a tickler chain. Stations were occupied at depths of 5, 9, 13, 14, 16, 22, 24, 27, 36, 47, 55, 64, 73, 82, 86, and 100 m. Collections were made during the day through September 1978; thereafter, a day and night cruise were usually made each month. The 22 m depth range was primarily occupied after October 1978, and depths >47 m were first occupied in June 1979. Two tows of 10 min bottom time were made at each depth except that 1 tow was made prior to October 1978, 8-12 tows were made at 14 m, and 24 tows usually were made at 22 m.

All *S. caprinus* were separated from the catch, measured for total length, fixed in 10% Forma-

[1]Based on a thesis submitted by the senior author in partial fulfillment for the M.S. degree, Texas A&M University.

[2]Technical Article 17149 from the Texas Agricultural Experiment Station, College Station, TX 77843.

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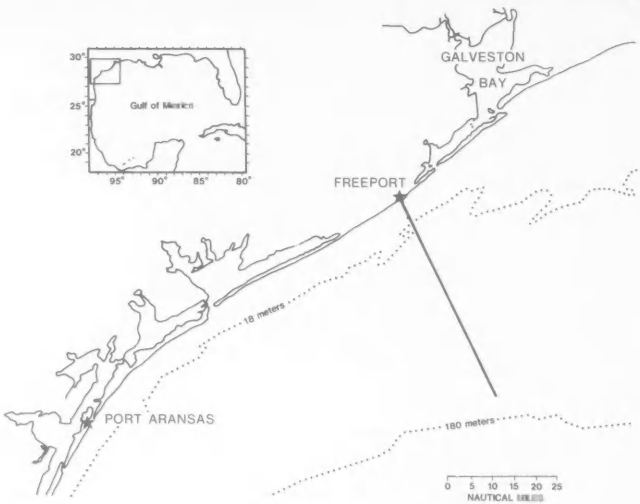


FIGURE 1.—Location of sampling areas with transect indicating stations occupied off Freeport, Tex.

lin,[6] and later preserved in 70% ethanol. For the period October 1978 to March 1980, 300 fish each month were selected by stratified random sampling to determine total length (TL), fork length (FL), standard length (SL), girth (G) at the fourth dorsal spine, total weight (TW), and ovary maturity stage and to take scale samples, except that only total weight, total length, sex, gonad weight, and ovary maturity stage were determined from October 1979 to March 1980. Female and immature fish were assigned gonad maturity stages (Table 1) similar to Kesteven's system (Bagenal and Braum 1971). Scales were taken below the lateral line near the tip of the pectoral fin following procedures for *S. chrysops* (Dery and Rearden[7]), and cellulose acetate impressions were examined using a scale projector.

Supplemental collections were made aboard the FRS *Oregon II* (NMFS) from 10 April to 1 May 1980 in the north central Gulf at depths of 9-91 m between long. 91°31′ and 92°00′W (Rohr et al.[8]). *Stenotomus caprinus* were selected from the catch without randomization procedures and measured in fork length.

TABLE 1.—Description of gonad maturity stages assigned to *Stenotomus caprinus*.

Stage	Description
1 Immature	Gonads barely or not visible.
2 Maturing virgin	Gonads very small, sexes not distinguishable.
3 Early developing	Sexes distinguishable but individual eggs are not visible.
4 Late developing	Eggs opaque, ovaries extending along <90% of gut cavity.
5 Gravid	Ovaries extend along 90% or more of lateral wall of gut cavity, < 50% of eggs translucent.
6 Ripe	Ovaries extend 90% or more of lateral wall of gut cavity, >50% of eggs translucent.
7 Spent/resting	Ovaries barely extend along lateral wall of gut cavity, flaccid with few small eggs. Similar in appearance to Stage 3, but occurs in fish large enough to have already spawned.

Year class identities were indicated by specifying the years in which the fish hatched. Age was determined by analysis of length frequencies, e.g., the Petersen method (Lagler 1956; Tesch 1971). The superior merits of this procedure for *S. caprinus* are noted in the section on Age Determination Using Scales. Size descriptions for each year class and each cruise (Table 2, Fig. 2) were based on major portions of frequency distributions cited. Boundaries between groups are indicated in Table 2 and Figure 2; mortality and growth calculations were based on groups defined by these boundaries. Arithmetic means were used to describe central tendencies for each year class and each cruise because length frequencies within year classes were

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Dery, L., and C. Reardon. 1979. Report of the State-Federal scup (*Stenotomus chrysops*) age and growth workshop. Woods Hole Lab. Ref. 79-57, 10 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[8]Rohr, B. A., A. J. Kemmerer, and W. H. Fox, Jr. 1980. FRS *Oregon II* Cruise 106 4/10-5/1/80. Cruise Report, 12 p. Southeast Fisheries Center Pascagoula Laboratory, National Marine Fisheries Service, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567.

approximately normally distributed. Hatching dates of 15 February and 15 March were assigned to the 1978 and 1979 year classes, respectively, to estimate their growth and ages. Descriptions of spawning periodicity and growth assume that *S. caprinus* reach 20-30 mm TL 1-2 mo after hatching. This assumption and assigned hatching dates seem reasonable because: 1) *Stenotomus caprinus* average 13-14 mm TL/30 d growth during their first 8 mo of life (Fig. 3); 2) the slope and elevation of the regression of ovary weight on total length for the 1979 year class was greatest in mid-March (Fig. 4, Table 3) and back calculated length of this year class was −5.26 mm TL at 0 d of age (Fig. 5). A hatching date of 15 February was assigned to the 1978 year class because this year class recruited about 1 mo earlier in 1978, although gonad data are lacking for this period. There appears to be no published data on size at early age other than our findings.

Our interpretations of the life history of *S. caprinus* obviously apply best to the area off Freeport, Tex., but they probably apply to much broader areas in the Gulf, judging from the agreement of our findings with the general published data on this species.

MATURATION AND SPAWNING SEASONALITY

Results

Stenotomus caprinus mature at 90-125 mm TL as they approach age I. Sex could be determined by eye at 90 mm TL as many fish entered the Early Developing stage (Fig. 6). Fish entered the Late Developing, Ripe, and Gravid stages at 100-125 mm TL. These data are supported by the extrapolated x-intercepts of ovary weight on total length which were 80-100 mm TL during the January-April spawning period (Fig. 4, Table 3). Our estimates of size at maturity agree with the mean sizes at age I given later.

Little somatic growth occurs after *S. caprinus* enters the later stages of gonad maturation (Fig. 6). Mean sizes of fish approaching age I were 110 mm TL in the Early Developing, 113 mm in the Late Developing, 115 mm in the Gravid and Ripe, and 118 mm in the Spent/Resting stages.

Stenotomus caprinus spawn once a year in a discrete period from January through April. This period is indicated by collections off Texas of fish that were 30-40 mm TL in April 1978, 20-50 mm in May 1979, and 20-40 mm in February-March 1980 (Fig. 2), and by the capture of fish 20-80 mm TL in late April 1980 in the north central Gulf (Fig. 7). No spawning occurs from May through December, because the smallest fish collected in that period belong to year classes hatched before May. Peak spawning occurred in March and early April in 1979 and from January through March 1980 as indicated by the increased slopes and elevated ovary weight-total length regression lines in those periods (Fig. 4, Table 3). The sharply defined and readily followed length-frequency modes for each year class indicate that spawning occurs in one discrete period each year.

Gonad maturity data support a January-April spawning period and indicate that virtually all *S. caprinus* spawn at 12 mo of age. Fish in Gravid or Ripe stages occurred only in the period January-April, and Spent/Resting stage fish appeared immediately thereafter (Fig. 8). Virtually all spawning occurs in the period January-April and few fish delay spawning until age II because extremely few fish were in the Immature, Maturing Virgin, or Early Developing stages in that period.

The spawning period probably spans about 50-80 d within the January-April interval, assuming larger fish were spawned before smaller ones, and all fish grew at the same rate as noted later. The spawning period duration was approximated from growth increments and size ranges (expressed as 99% confidence limits for observations) of the 1978 and 1979 year classes in June and July (Table 2), their first months of full recruitment. The mean 99% confidence limit for observations in the June-July period was 22.19 mm in 1978 and 40.27 mm in 1979, and respective mean daily growth was 0.45 mm/d and 0.50 mm/d. Calculated lengths of spawning periods were 49 d in 1978 (22.19 mm ÷ 0.45 mm/d) and 82 d in 1979 (40.85 mm ÷ 0.50 mm/d). These estimates suggest that the successful spawning period is much shorter than the January-April interval indicated by length compositions and gonad data.

Stenotomus caprinus exhibited a sex ratio of 1.00 male to 1.21 females. This ratio was observed in 1,506 fish examined during the spawning period and differs significantly from 1:1 ($\chi^2 = 13.01$, $\alpha = 0.05$, df = 1).

Discussion

Our findings agree with the limited literature on *Stenotomus* reproduction. Previous workers

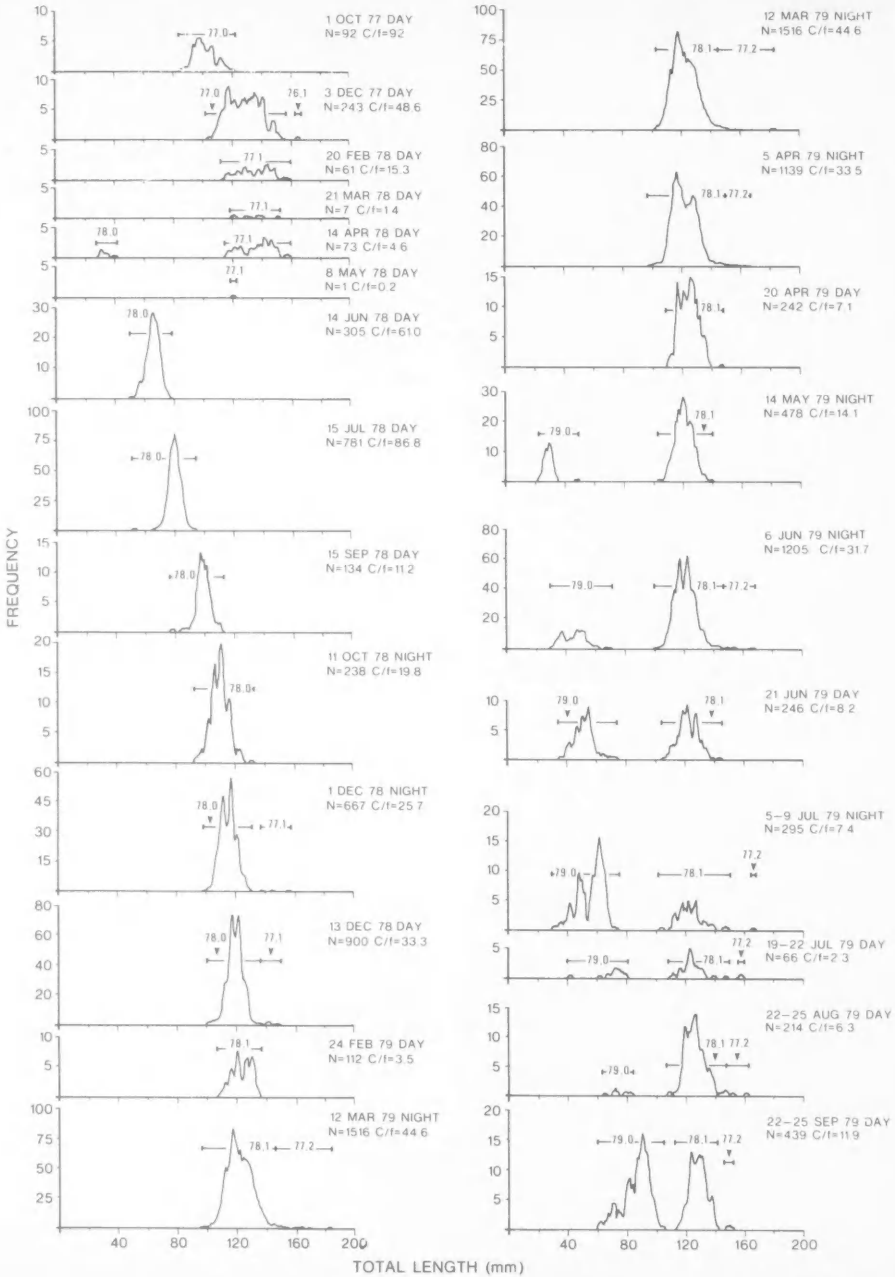
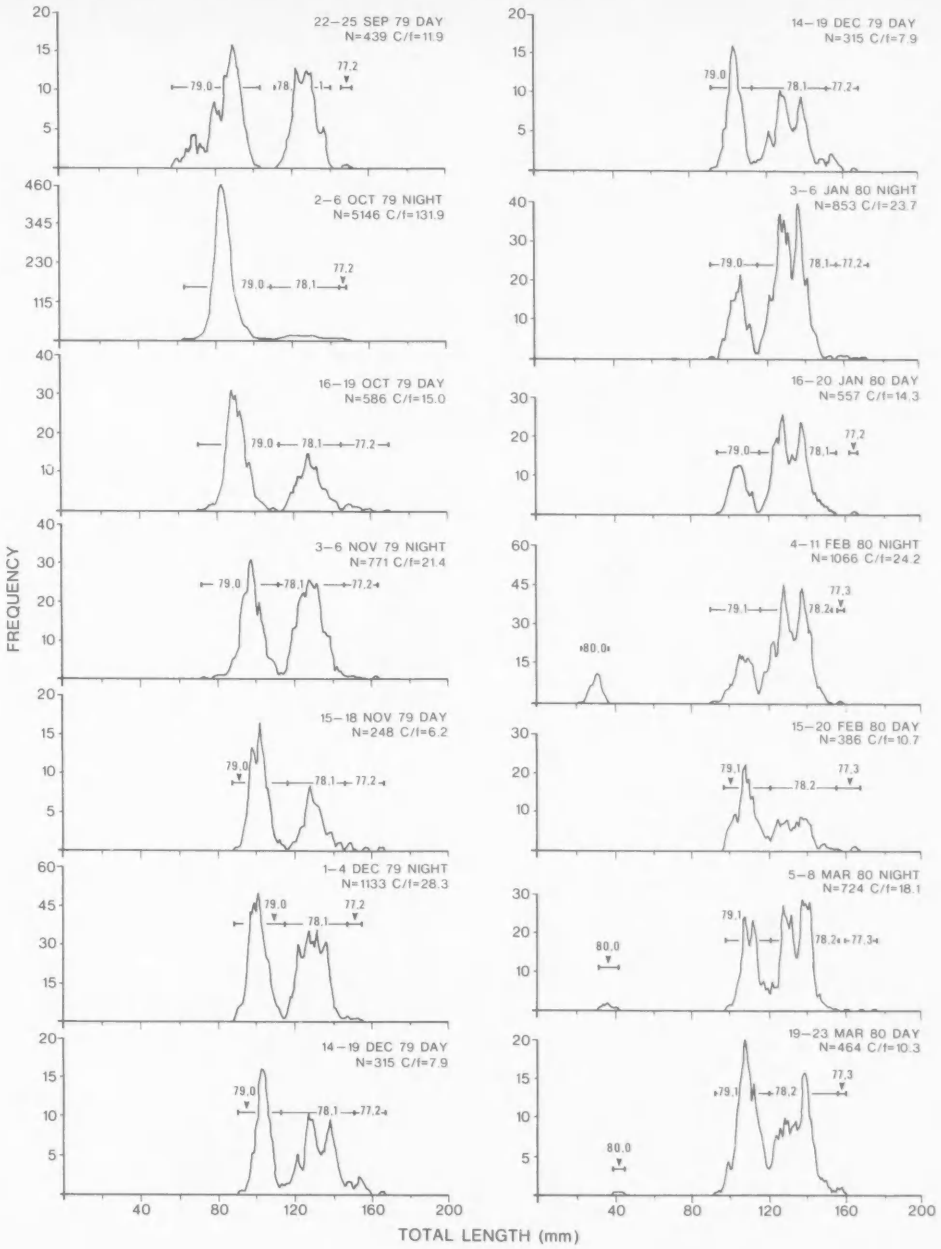


FIGURE 2.— Monthly length frequencies (moving averages of three) of *Stenotomus caprinus* off Freeport, Tex. Bars in each panel



indicate the size range of a year class. The first two digits within a bar indicate the year class; the last digit is age in years; e.g., 78.1 represents the 1978 year class when age I. C/f indicates number of individuals per 10-min tow.

TABLE 2.—Growth data (mm TL) for *Stenotomus caprinus* from the Gulf off Freeport, Tex. Increments with an asterisk (*) were adjusted to growth per 30 d and plotted in Figure 3. Night and day cruises are indicated by N and D. Observed size ranges delineate year class boundaries used in growth and mortality calculations.

Collection date	*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
			1977 Year Class				
1 Oct. 1977, D	92	85-120	100.5	54.1	99.0-102.0	81.3-119.4	
5 Nov. 1977, D	0	—	—	—	—	—	—
3 Dec. 1977, D	242	103-157	127.6	123.3	126.2-129.0	99.0-156.2	+27.1
20 Feb. 1978, D	61	113-157	134.4	125.0	131.6-137.2	105.6-163.2	+6.8
21 Mar. 1978, D	7	119-150	132.0	116.0	122.4-141.6	94.3-169.7	−2.4
14 Apr. 1978, D	66	95-157	135.9	115.2	133.3-138.5	108.3-163.5	+3.9
8 May 1978, D	1	120	120.0	0	120.0	120.0	−15.9
14 June 1978, D	0	—	—	—	—	—	
15 July 1978, D	0	—	—	—	—	—	
15 Sept. 1978, D	0	—	—	—	—	—	
11 Oct. 1978, N	0	—	—	—	—	—	
1 Dec. 1978, N	3	136-155	145.3	82.3	128.6-162.0	92.3-198.3	+25.3
13 Dec. 1978, D	12	136-147	141.2	11.1	139.1-143.3	131.0-151.4	−4.1
24 Feb. 1979, D	0	—	—	—	—	—	
12 Mar. 1979, N	15	146-182	155.8	99.2	150.3-161.3	126.4-185.2	+14.6
5 Apr. 1979, N	7	151-165	156.4	22.3	152.2-160.6	139.9-172.9	+0.6
20 Apr. 1979, D	0	—	—	—	—	—	
14 May 1979, N	0	—	—	—	—	—	
5 June 1979, N	10	145-166	154.6	40.9	150.1-159.1	134.3-174.9	−1.8
21 June 1979, D	0	—	—	—	—	—	
5 July 1979, N	1	165	165.0	0	165.0	165.0	+11.4
19 July 1979, D	3	145-157	153.0	37.0	141.8-164.2	117.5-188.5	−12.0
22 Aug. 1979, D	3	146-159	151.7	44.3	139.5-163.9	112.8-190.6	−1.3
22 Sept. 1979, D	2	146-148	147.0	2.0	110.1-183.9	133.1-160.9	−4.7
2 Oct. 1979, N	4	145-160	153.0	38.7	144.4-161.6	124.4-181.6	+6.0
16 Oct. 1979, D	19	145-167	151.7	34.3	148.9-154.5	134.9-168.5	−1.3
3 Nov. 1979, N	6	144-161	149.8	38.2	143.6-150.0	126.9-172.7	−1.9
15 Nov. 1979, D	5	144-164	152.4	56.3	143.8-161.0	122.1-182.7	+2.6
1 Dec. 1979, N	12	144-153	148.7	7.9	146.9-150.5	140.1-157.3	−3.7
14 Dec. 1979, D	4	150-164	157.6	19.7	151.3-163.7	137.1-177.9	+8.8
3 Jan. 1980, N	8	154-170	161.5	20.3	156.8-165.2	146.4-176.6	−4.0
16 Jan. 1980, D	1	164	164.0	0	164.0	164.0	+2.5
4 Feb. 1980, N	2	155-157	156.5	0.5	154.3-158.7	149.5-163.5	−7.5
15 Feb. 1980, D	4	156-165	162.2	17.6	155.4-168.0	142.9-181.5	+5.7
5 Mar. 1980, N	4	154-175	164.5	77.7	152.3-176.7	116.1-205.1	+2.3
19 Mar. 1980, D	3	155-158	156.7	1.3	154.6-158.8	150.0-163.4	−7.8
			1978 Year Class				
14 Apr. 1978, D	7	29- 40	32.3	11.9	29.2- 35.4	20.2- 44.4	
8 May 1978, D	0	—	—	—	—	—	
14 June 1978, D	305	50- 76	64.9	19.5	64.4- 65.4	53.5- 76.3	+32.6*
15 July 1978, D	781	51- 93	79.0	17.6	78.7- 79.3	68.2- 89.8	+14.1*
15 Sept. 1978, D	134	78-111	98.7	25.4	97.8- 99.6	85.7-111.7	+19.7*
11 Oct. 1978, N	238	93-131	109.2	35.8	108.4-110.0	93.8-124.6	+10.5*
1 Dec. 1978, N	664	98-135	114.3	28.2	113.9-114.7	100.6-128.0	+5.1*
13 Dec. 1978, D	888	100-135	117.8	26.9	117.5-118.1	104.4-131.2	+3.5*
24 Feb. 1979, D	112	107-133	121.8	40.9	120.6-123.0	105.3-138.3	+4.0*
12 Mar. 1979, N	1,501	96-145	120.7	65.1	120.3-121.1	99.9-141.5	−1.1*
5 Apr. 1979, N	1,132	98-150	121.4	64.9	120.9-121.9	100.6-142.2	+7.0*
20 Apr. 1979, D	241	110-146	123.5	39.7	122.7-124.3	107.3-139.7	+2.1*
14 May 1979, N	389	100-138	119.8	33.7	118.9-120.7	104.8-134.8	−3.7*
6 June 1979, N	988	100-144	119.5	48.9	119.4-119.6	101.5-137.5	−0.3*
21 June 1979, D	135	100-143	121.7	47.3	120.5-122.9	104.0-139.4	+2.2*
5 July 1979, N	73	101-145	121.4	59.2	120.9-121.9	101.6-141.2	−0.3*
19 July 1979, D	46	110-144	122.2	34.2	120.5-123.9	106.4-138.0	+0.8*
22 Aug. 1979, D	202	105-145	124.4	42.3	123.5-125.3	107.6-141.2	+2.2*
22 Sept. 1979, D	190	110-145	125.6	30.4	124.8-126.4	111.4-139.8	+1.2*
2 Oct. 1979, N	209	110-144	124.7	50.5	123.7-125.7	106.4-143.0	−0.9*
16 Oct. 1979, D	212	113-144	127.6	38.7	126.8-128.4	111.6-143.6	+3.6*
3 Nov. 1979, N	410	116-143	127.3	35.9	126.7-127.9	111.9-142.7	−0.3*
15 Nov. 1979, D	88	116-143	128.6	37.9	127.3-129.9	112.7-144.5	+1.3*
1 Dec. 1979, N	608	116-143	129.0	45.1	128.5-129.5	111.7-146.3	+0.4*
14 Dec. 1979, D	175	116-149	131.9	71.9	130.6-133.2	110.1-153.7	+2.9*
3 Jan. 1980, N	647	116-153	131.6	48.3	131.1-132.1	113.7-149.5	−0.3*
16 Jan. 1980, D	418	116-155	131.4	54.8	130.7-132.1	112.3-150.5	−0.2*
4 Feb. 1980, N	769	116-154	131.3	54.0	130.8-131.6	112.4-150.2	−0.1*
15 Feb. 1980, D	153	120-155	132.2	44.1	131.2-133.4	115.2-149.4	+1.0*
5 Mar. 1980, N	464	120-153	133.9	44.0	133.3-134.5	116.8-151.0	+1.6*
19 Mar. 1980, D	234	120-154	133.7	53.6	132.8-134.6	114.8-152.6	−0.2*

TABLE 2.—*Continued.*

Collection date	*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
			1979 Year Class				
14 May 1979, N	89	22- 49	27.6	10.5	26.9- 28.3	19.3- 35.9	
6 June 1979, N	207	29- 69	43.7	59.0	42.7- 44.7	23.9- 63.5	+16.1*
21 June 1979, D	111	35- 74	50.8	44.3	50.2- 51.4	33.7- 67.9	+7.1*
5 July 1979, N	220	30- 76	55.0	74.1	73.0- 75.2	32.8- 77.2	+4.2*
19 July 1979, D	17	40- 80	69.2	76.9	64.7- 73.7	46.6- 91.8	+14.2*
22 Aug. 1979, D	9	63- 81	72.9	33.1	68.8- 77.2	58.1- 87.7	+3.7*
22 Sept. 1979, D	247	58-102	83.3	78.8	77.7- 79.9	60.4-106.2	+10.4*
2 Oct. 1979, N	4,933	58-109	83.7	24.3	83.6- 83.8	71.0- 96.4	+0.4*
16 Oct. 1979, D	363	70-112	89.4	50.9	88.7- 90.1	71.0-107.8	+5.7*
3 Nov. 1979, N	355	72-115	96.8	36.5	96.2- 97.4	81.2-112.4	+7.4*
15 Nov. 1979, D	155	87-115	100.4	18.0	99.7-101.1	89.5-111.3	+3.6*
1 Dec. 1979, N	525	88-115	100.5	21.3	100.1-100.9	88.6-112.4	+0.1*
14 Dec. 1979, D	136	91-115	102.6	15.9	101.9-103.3	92.3-112.9	+2.1*
3 Jan. 1980, N	198	91-115	104.6	17.8	104.0-105.2	93.7-115.5	+2.0*
16 Jan. 1980, D	138	94-115	104.1	16.4	103.4-104.8	93.7-114.5	+0.5*
4 Feb. 1980, N	223	91-115	105.7	23.3	105.1-106.3	93.3-118.1	+1.6*
15 Feb. 1980, D	223	96-119	107.3	25.3	106.6-108.0	94.3-120.3	+1.6*
5 Mar. 1980, N	243	98-119	109.4	17.7	108.9-110.0	98.6-120.2	+2.1*
19 Mar. 1980, D	225	96-119	107.7	27.4	107.0-108.4	94.2-121.2	−1.7*

proposed a spring or late winter-early spring spawning period (Hildebrand 1954; Miller 1965; Chittenden and McEachran 1976) based on the captures of fish 106-159 mm TL with well-developed gonads in February (Hildebrand 1954) and fish 31-89 mm TL in early May and June (Caldwell 1955; Miller 1965). Henwood's (1975) histological studies indicated spawning from November through April, but our data indicate little or no spawning before January. Our finding that

TABLE 3.—Analyses of the monthly regressions of ovary weight (Y) in grams on total length (X) in millimeters for female *Stenotomus caprinus*, December 1978-March 1980. Regressions were significant (at $\alpha = 0.05$) except on 11 October 1978, 6 June 1979, 19 July 1979, 22 August 1979, and 22 September 1979.

Cruise	*n*	100 r^2	Equation
1 Dec. 1978	144	23.70	$Y = -0.963 + 0.010\,X$
24 Feb. 1979	41	17.89	$Y = -0.913 + 0.016\,X$
12 Mar. 1979	168	37.35	$Y = -3.096 + 0.038\,X$
5 Apr. 1979	109	48.18	$Y = -3.295 + 0.036\,X$
20 Apr. 1979	84	7.00	$Y = -0.496 + 0.008\,X$
14 May 1979	110	23.26	$Y = -0.166 + 0.002\,X$
5 July 1979	24	36.97	$Y = -0.333 + 0.004\,X$
2 Oct. 1979	79	41.52	$Y = -0.352 + 0.004\,X$
16 Oct. 1979	53	10.58	$Y = -0.109 + 0.002\,X$
3 Nov. 1979	89	47.78	$Y = -0.232 + 0.003\,X$
15 Nov. 1979	65	58.86	$Y = -0.564 + 0.007\,X$
1 Dec. 1979	68	71.36	$Y = -1.486 + 0.016\,X$
14 Dec. 1979	83	62.26	$Y = -1.450 + 0.016\,X$
3 Jan. 1980	97	51.04	$Y = -1.613 + 0.020\,X$
16 Jan. 1980	85	82.36	$Y = -2.329 + 0.026\,X$
4 Feb. 1980	93	73.57	$Y = -3.132 + 0.036\,X$
15 Feb. 1980	79	59.02	$Y = -1.962 + 0.024\,X$
5 Mar. 1980	81	48.07	$Y = -2.203 + 0.028\,X$
19 Mar. 1980	64	69.22	$Y = -2.148 + 0.026\,X$

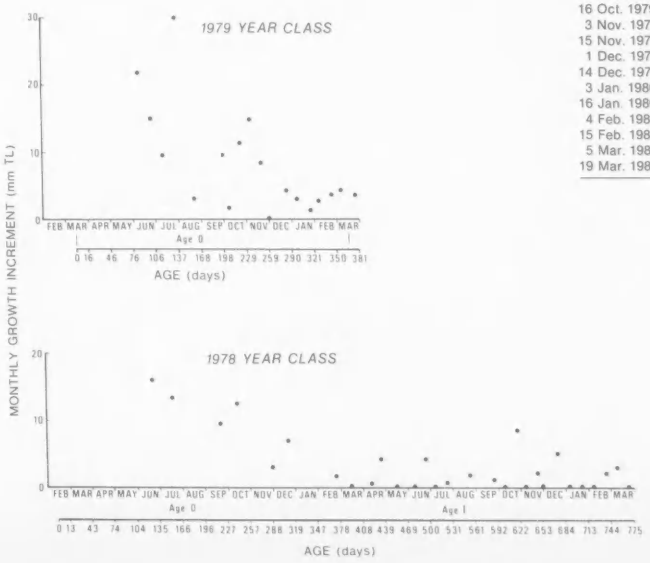


FIGURE 3.—Monthly growth increments for the 1978 and 1979 year classes of *Stenotomus caprinus*. Unadjusted growth increments (Table 2) were converted to growth per 30 d. Negative growth was rounded to 0.

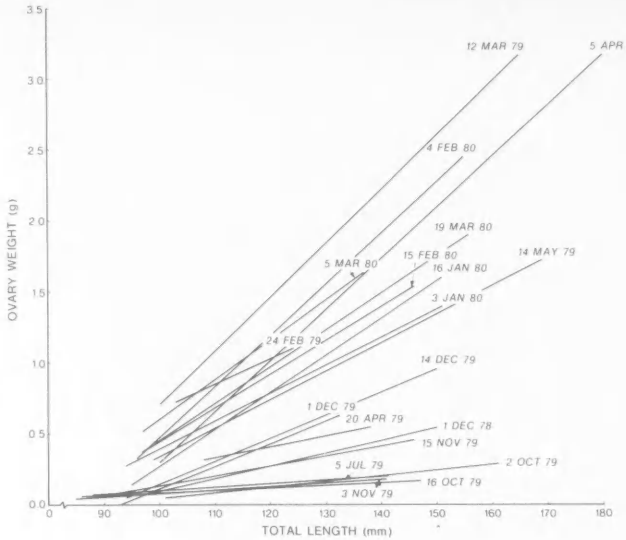


FIGURE 4.—Monthly ovary weight-total length regressions for *Stenotomus caprinus*. The length of each line shows the observed size range.

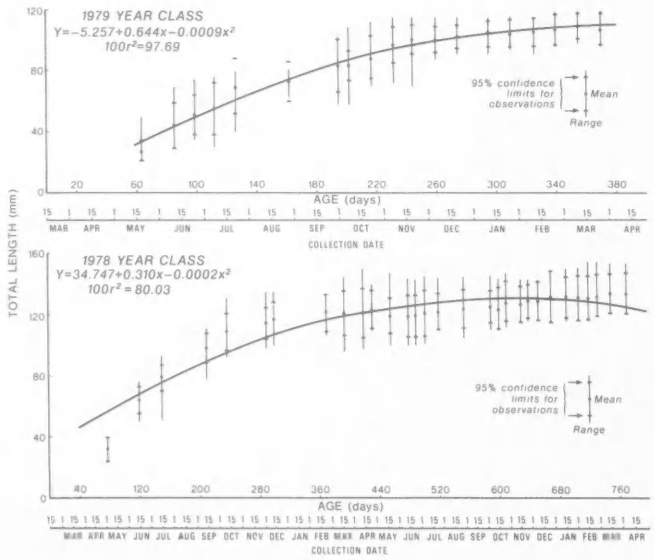


FIGURE 5.—Mean observed and predicted sizes at age for the 1978 and 1979 year classes of *Stenotomus caprinus*. Mean sizes at age (Table 2) were regressed on age after assigned hatching dates of 15 February and 15 March for these respective year classes. Regressions were significant at $\alpha = 0.05$.

virtually all *S. caprinus* spawn at 12 mo of age has not been reported, nor has the discrete and short duration of spawning been recognized. Sex ratios have not been reported for *S. caprinus*, although 1:1 and 1:1.26 male to female ratios have been reported for its congener *S. chrysops* (Smith and Norcross 1968; Morse 1978). The pattern of spawning in *S. caprinus* is several months earlier in timing but similar to *S. chrysops* which spawns once a year from May through August

with greatest spawning in June (Bigelow and Schroeder 1953; Finkelstein 1969a).

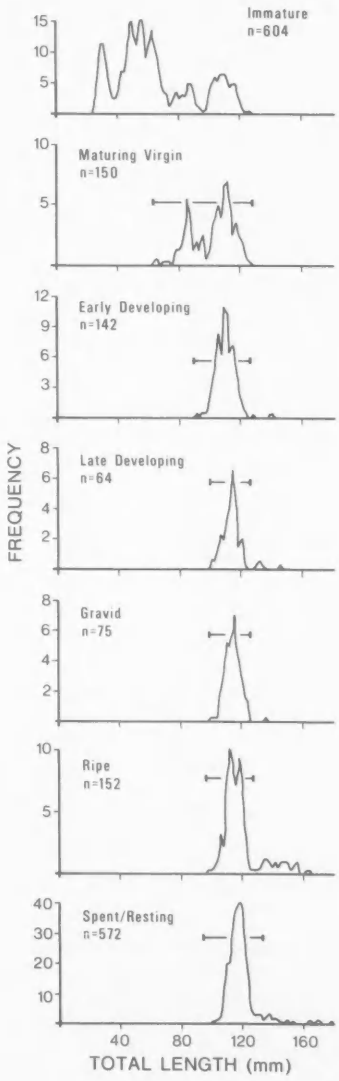


FIGURE 6.—Length frequencies (moving averages of three) of immature and female *Stenotomus caprinus* by maturity stages. See Table 1 for definitions of maturity stages. Brackets indicate size ranges used to calculate the mean length of fish approaching age I for each maturity stage.

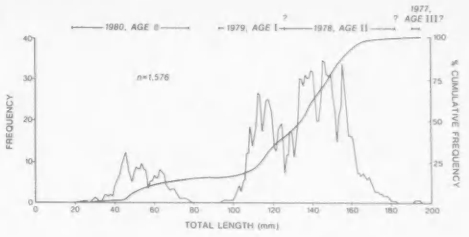


FIGURE 7.—Length frequency (moving averages of three) of *Stenotomus caprinus* captured in the north central Gulf aboard the *Oregon II*, 10 April-1 May 1980. Probable ages and year class identities are indicated.

MOVEMENTS, SPAWNING AREAS, AND DIEL VARIATION IN CATCH

Results

Stenotomus caprinus exhibit size and age gradients with depth related to their movements, spawning areas, and recruitment. Although captured from 18 m to 100 m (Fig. 9), they were most common between 36 m and 55 m.

Young-of-the-year recruited in inshore waters during the spring and moved towards deeper water as they grew. Recently hatched fish 20-50 mm TL appeared only in 18-27 m depths in the period February-May (Fig. 9), but became distributed as deep as 36-47 m by June to September. The larger young-of-the-year continued to disperse gradually to deeper water as indicated by their size gradients with depth in June-September 1979 and in October 1979-January 1980.

Adult *S. caprinus* reside and spawn in waters deeper than 27 m. No adults were found in waters shallower than 27 m during the January-April spawning period (Fig. 9). Fish of ages I and II occurred in waters deeper than 27 m throughout the year but showed no size gradient with depth. This indicates that they were uniformly mixed throughout the 27-100 m depth range.

Stenotomus caprinus appear most vulnerable to trawling at night. Mean catch per tow at night in the 18-100 m depth range that *S. caprinus* occupies averaged three times that of day catches on 10 of 11 occasions in the period December 1978-March 1980 when day and night cruises were made each month or close together in time (Fig. 2).

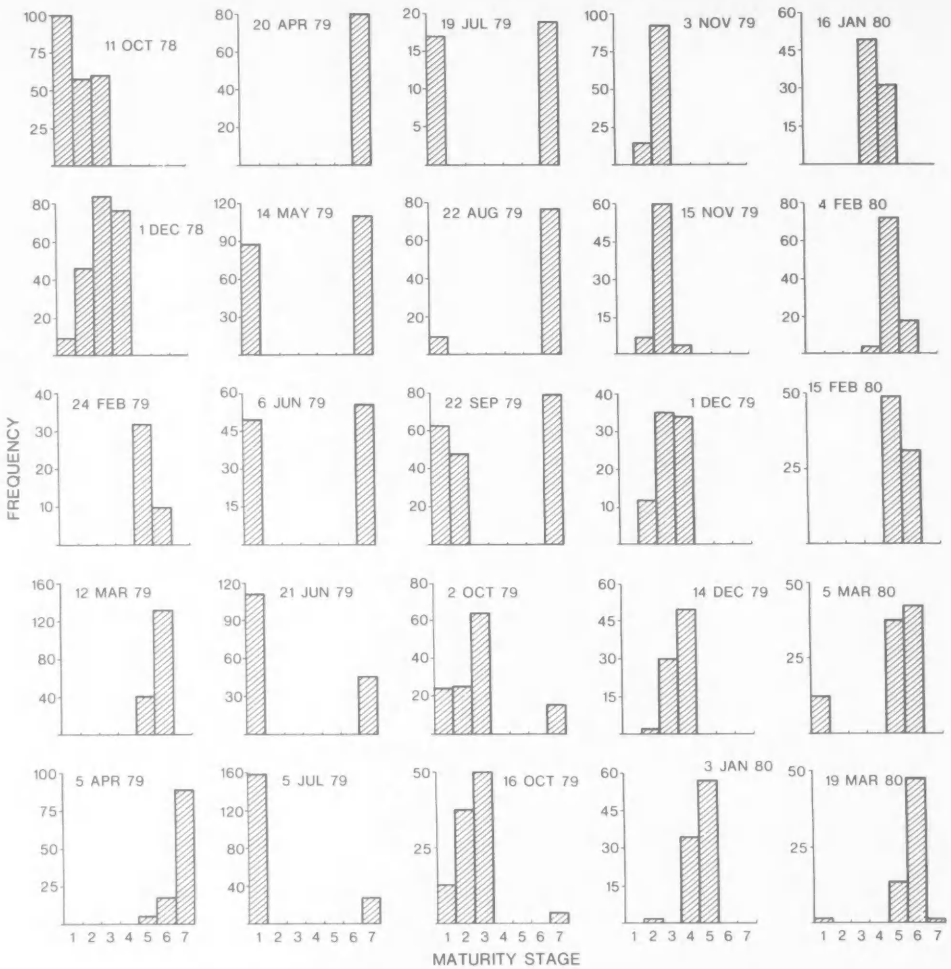


FIGURE 8.—Monthly maturity stages of female *Stenotomus caprinus*. Maturity stages are described in Table 1.

Discussion

The spawning periodicity of *S. caprinus* appears timed to coincide with the late winter-early spring periodicity of onshore surface currents on the continental shelf of the northwestern Gulf. Rising sea levels in the period January-April (Marmer 1954) coincide with onshore surface currents (Kimsey and Temple 1963; Smith 1975). This current system could transport eggs and larvae from offshore spawning areas to inshore nurseries where the young recruit, assuming that *S. caprinus* have pelagic eggs and larvae like *S. chrysops* (Johnson 1978).

Our findings on the movements and distribution of *S. caprinus* agree with the literature. The size-depth relationship in which younger individuals occur inshore in the spring has been reported (Hildebrand 1954; Caldwell 1955; Miller 1965). Our findings on size-depth gradients during the summer support Henwood's (1975) suggestion that young-of-the-year gradually dis-

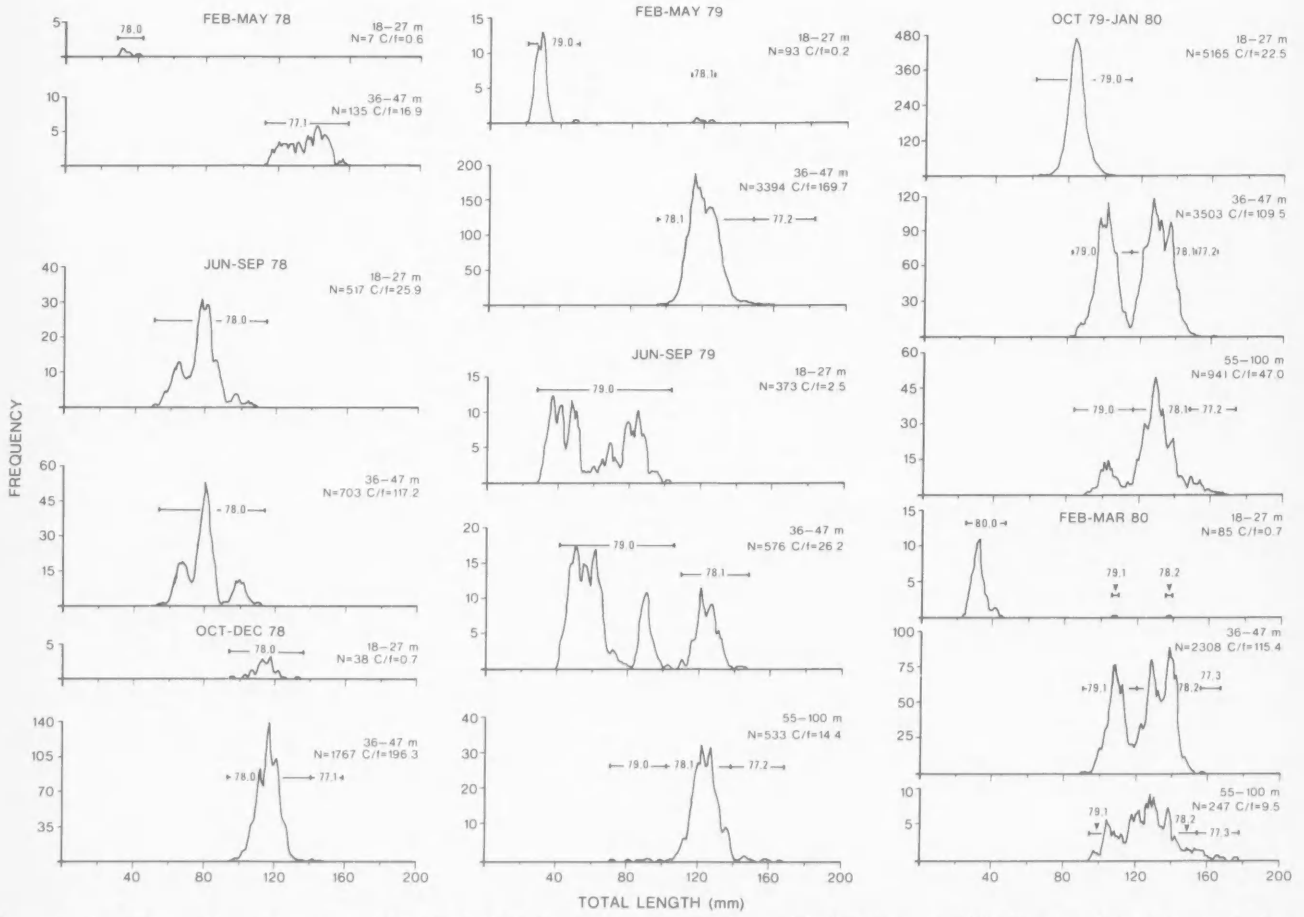


FIGURE 9.—Length frequencies (moving averages of three) by depth for *Stenotomus caprinus* off Freeport, Tex. Multiple peaks within size ranges designated as age 0 reflect growth. C/f indicates number of individuals per 10-min tow.

perse to deeper water. Our finding that age-I and age-II fish show no size-depth gradient and are mixed throughout 27-100 m depths has not been reported but agrees with Moore's (1964) finding that average weight did not increase in waters deeper than 64 m.

Our findings that *S. caprinus* is most vulnerable to trawling at night has not been reported, although similar behavior has been recorded for *S. aculeatus* (Powles and Barans 1980). Fritz (1965) found that *S. chrysops* made up a greater percentage of the catch at night, although Smith and Norcross (1968) reported crepuscular catches were greatest. Henwood et al. (1978) suggested that *S. caprinus* actively feeds during the day. These fish might be inactive and near the bottom at night, and thus more vulnerable to trawling.

AGE DETERMINATION USING SCALES

Results

Stenotomus caprinus cannot be aged readily using scales. Scales from 2,342 fish were examined for annuli using criteria of Dery and Rearden (footnote 7) which include cutting over, irregular spacing, and breaking of circuli. Marks similar to annuli were occasionally observed, but these marks varied greatly between scales from the same fish and between fish of the same size, age by length-frequency analysis, and date of capture. Annuli frequently were not apparent on fish that must have been age II or III according to length-frequency analysis, although one important criterion for valid use of the scale method (Lagler 1956; Tesch 1971) is that this procedure should agree with ages determined from length frequencies.

Discussion

Our finding that it is difficult to age *S. caprinus* using scales agrees with Henwood (1975). In contrast, several authors have used scales successfully to age *S. chrysops* (Finkelstein 1969a; Hamer 1979[9]); although this becomes difficult beyond age III (Smith and Norcross 1968).

Stenotomus caprinus are best aged using length frequencies, particularly if, as in the present study, there is a long-term set of data from cruises made close together in time. Under these conditions age determination by length-frequency analysis may be obvious, as we found. Length-frequency analysis would be less reliable if cruises were several months apart in time, because year class frequencies could merge after age I as our data indicate. The superior merits of age determination by length-frequency analysis are not surprising for *S. caprinus* because 1) this species spawns once a year in a discrete period, 2) within year class frequencies appear normally distributed, and 3) growth of large and small fish within a year class is uniform as evidenced by the observed constant variance. In addition, length-frequency analysis generally is most clear for younger ages (Lagler 1956; Tesch 1971), and *S. caprinus* only lives a few years (see section on Mortality and Postspawning Survival).

AGE DETERMINATION AND GROWTH USING LENGTH-FREQUENCY ANALYSIS

Results

No more than four year classes of *S. caprinus* were present at any time off Texas and only one or two predominated. These year classes represented young-of-the-year and ages I, II, and III (Fig. 2). Only one year class predominated in any month from October 1977 through April 1979, although two year classes often were captured. The 1977 year class predominated initially in this period but virtually disappeared at age I after the 1978 year class recruited. Three year classes usually were captured after the 1979 year class recruited in May. In contrast to the virtual disappearance of the 1977 year class, the 1978 year class remained abundant at age I after the new year class recruited. As a result, two year classes (1978 and 1979) were equally predominant from May 1979 through March 1980. Four year classes were present after the 1980 year class recruited in February, but only the 1978 and 1979 year classes predominated.

Minor qualifications should be noted to the designation of the 1977 year class. The group identified as the 1977 year class in the period December 1977-April 1978 may contain members of the 1976 year class. This is suggested because 1) the size range of fish in that period may be too broad for one year class; 2) apparent

[9]Hamer, P. 1979. Studies of the scup, *Stenotomus chrysops*, in the Mid-Atlantic Bight. N.J. Div. Fish, Game, Shellfish., Necote Creek Res. Stn., Misc. Rep. 18m, 66 p.

growth between October and December 1977 is high when compared with the same period in other years; and 3) size at age I is comparatively large for the 1977 year class. The 1977 and 1978 year classes were difficult to distinguish after December 1978, so that the 1977 year class thereafter may include fast growing members of the 1978 year class.

Stenotomus caprinus growth varied between year classes, but sizes averaged 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. Observed mean sizes at age I, based on pooled data from February and March (Table 2), were 134.2 mm TL for the 1977 year class (range 113-157 mm), 120.8 mm for the 1978 year class (range 96-145 mm), and 107.5 mm for the 1979 year class (range 91-119 mm). These sizes at age I agree with regression predictions (Fig. 5) of 114.8 mm TL for the 1978 year class and 110.0 mm for the 1979 year class. Observed mean size at age II was 132.5 mm TL for the 1978 year class (range 116-155) (Table 2), which closely agrees with a regression prediction of 128.6 mm (Fig. 5). The few survivors of the 1977 year class averaged 155.8 mm TL (range 146-182) at age II and 160.8 mm at age III (range 154-175 mm) (Table 2). Many fish approached the maxima in the size ranges at age cited for each year class, and the ranges at age appeared constant between collections indicating uniform growth (Table 2).

Possible error in assigned hatching dates would have little effect on our estimates for mean sizes at age because 99% confidence intervals of observations were constant within the following periods (Table 2): December 1977-April 1978 for the 1977 year class; December 1978-June 1979 for the 1978 year class; and December 1979-March 1980 for the 1979 year class.

Stenotomus caprinus grow rapidly in their first 8 mo, but growth slows greatly as they mature and appears negligible after maturity. The 1978 and 1979 year classes showed a rapid, almost linear decline in monthly growth increments during their first 8 mo (Fig. 3). Growth of the 1978 year class averaged 13.62 mm TL/30 d from 15 February through early October 1978, and the 1979 year class averaged 12.66 mm/30 d from 15 March to early November 1979, ignoring the regression effect. In contrast, the 1978 year class grew only 13 mm TL in its second year; and the 1977 year class grew only 23 mm in its second year and 4 mm in its third year. This growth pattern may result in gradual merging of year class size compositions after age I as indicated by the 1978 and 1979 year classes (Fig. 2). The small amount of growth after maturity seems to occur primarily during the late spring-early fall interim between reproductive activities (Fig. 3). Very little growth occurred in the January-April spawning period when the 1978 year class averaged 0.83 mm TL/30 d in that period in 1979 and 0.80 mm/30 d in 1980.

Size at age I varies between *S. caprinus* year classes, but growth is not obviously density dependent. No simple relationship was apparent for the 1977-79 year classes (Fig. 10) between mean size at age I and their index of year class strength, calculated as $\Sigma c_i/\Sigma f_i$ where Σf_i is the total number of tows and Σc_i is the total catch at age I for each year class at depths of 27-47 m. Fish of the weak 1979 year class averaged smaller at age I (107.5 mm TL) than the strong 1978 year class (120.8 mm), a pattern not consistent with density dependent growth. Growth of the 1979 year class might have been depressed by interaction with the strong 1978 year class, but no density dependent relationship was apparent even when a pooled index of population strength was substituted for the 1979 year class strength index.

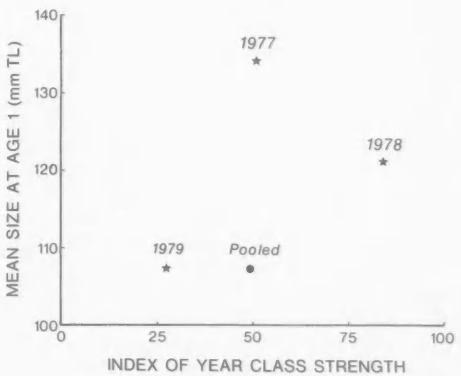


FIGURE 10.—Relationship between mean sizes at age I and year class strength for *Stenotomus caprinus* off Freeport, Tex. Indices of individual year class strength are indicated by stars and the pooled index by solid circle.

Discussion

Our findings on growth are largely new because the growth of *S. caprinus* has not been described previously. Sizes at age I agree with Chittenden and McEachran's (1976) suggestion

that *S. caprinus* reaches 90-123 mm TL at age I. Back-calculated lengths of *S. chrysops* are 120-155 mm TL at age I and 182-213 mm at age II (Finkelstein 1969a; Hamer footnote 9). Sizes at age I appear to be similar in these species, but *S. chrysops* is much larger at age II. Our growth data and the constant size noted in later gonad maturity stages (Fig. 6) indicate that *S. caprinus* markedly diverts energy from somatic growth to gonadal development as it matures. The different sizes of these congeners at age II probably reflect this drastic diversion of energy in *S. caprinus*.

MAXIMUM SIZE AND LIFESPAN

Results

The maximum size typically reached by *S. caprinus* is about 200 mm TL. The largest fish collected off Texas ($n = 22,924$) was 182 mm TL, and the largest specimen collected in the north central Gulf ($n = 1,576$) aboard the *Oregon II* was 193 mm TL.

The maximum lifespan of *S. caprinus* typically appears to be 2.5-3 yr. In the period October 1977-March 1980, 99% of the specimens captured off Texas were <146 mm TL, and 99.5% were <149 mm (Fig. 11). Many age II fish captured off Texas were as large as 155 mm TL. The largest fish collected was age II when captured in March 1979, or age III if it was a member of the poorly defined 1976 year class (Fig. 2). These data indicate that a value of $t_L = 2.5$-3 yr is reasonable for this Beverton-Holt model parameter (Gulland 1969). This estimate is supported by data from the north central Gulf (Fig. 7) in which 99% of the fish were <172 mm TL and 99.5% were <176 mm. Fish of these sizes were age II or III in the north central Gulf (Fig. 7).

Discussion

The maximum sizes reported herein are slightly larger than the maximum size reported by Hildebrand (1954), Caldwell (1955), and Chittenden and McEachran (1976). The only published record of *S. caprinus* much larger than 200 mm TL is that of Franks et al. (1972) who captured a specimen 256 mm TL in the north central Gulf. The apparent larger size of individuals at given percentages of the catch in the north central Gulf might reflect growth differences between areas, or the nonrandom sub-

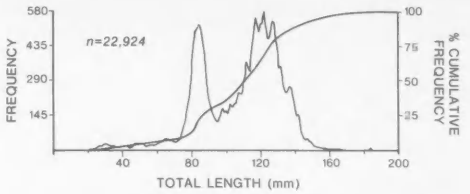


FIGURE 11.—Length frequency (moving averages of three) and cumulative percent frequency of all *Stenotomus caprinus* collected off Freeport, Tex., October 1977-March 1980.

sampling from the *Oregon II* catch which would probably select larger fish. Values of t_L would vary from year to year due to variation in postspawning survival noted later.

MORTALITY AND POSTSPAWNING SURVIVAL

Results

Stenotomus caprinus has a total annual mortality rate of about 83-99% on a time-specific basis. Time-specific total annual mortality rates ($1 - S$) were calculated from the expression $S = N_t/N_0$ where S = rate of survival, and N_t and N_0 are the numbers of fish collected at age each cruise in depths of 18-100 m. The pooled estimate, using Heincke's procedure (Ricker 1975) was 98.95% comparing the 1977 and 1978 year classes and individual rates generally exceeded 98%. These values probably overestimate $1 - S$, because the 1978 year class was stronger than the 1977 year class (Fig. 10). The pooled estimate comparing the apparent 1976 and 1977 year classes was 99.79%. The pooled estimate comparing the 1978 and 1979 year classes was 84.94% which may be fortuitous because it included one data set (October 1979) for which an exceptionally large number of fish from the 1979 year class were captured. A minimum pooled mortality estimate for the 1978 and 1979 year classes is 40.73%, if the exceptional October 1979 data set is excluded. This is probably a large underestimate because the 1979 year class was so much weaker than the 1978 year class. Realistic estimates could not be calculated in most instances comparing the 1978 and 1979 year classes because N_t exceeded N_0, which largely reflects the much greater strength of the 1978 year class (Fig. 10). Time-specific mortality estimates made from Chittenden and McEachran's (1976)

raw data were 99% for late September 1973 ($S = 5/435$) and 83% for January 1974 ($S = 395/2,468$). Pooled cohort-specific estimates of $1 - S$ were 99.23% for the 1977 year class and 83.36% for the 1978 year class using Heincke's procedure. The different mortality rates for these year classes are consistent with theoretical mortality rates given later, and the greater postspawning survival of the 1978 year class.

Postspawning survival of *S. caprinus*, total annual mortality rates, and maximum lifespan varies greatly between years and year classes. The 1977 and apparently 1976 year classes rarely appeared after they spawned at age I (Fig. 2). In contrast, many members of the 1978 year class survived after spawning at age I and spawned again at age II. White and Chittenden (1977) suggested somatic weight variation as a factor in the survival of the Atlantic croaker, *Micropogonias undulatus*. Somatic weight of female *S. caprinus* did not change in a regular monthly pattern, and regression elevations differed widely in consecutive months (Fig. 12, Table 4).

TABLE 4.—Analyses for the monthly regressions of somatic weight (Y) in grams on total length (X) in millimeters for female *Stenotomus caprinus*, October 1978-March 1980. All regressions were significant at $\alpha = 0.05$.

Collection date	n	100 r^2	Equation
11 Oct. 1978	53	86.01	$Y = -50.789 + 0.699\ X$
1 Dec. 1978	144	87.44	$Y = 71.240 - 1.323\ X + 0.008\ X^2$
24 Feb. 1979	41	78.88	$Y = -32.009 + 0.506\ X$
12 Mar. 1979	168	94.57	$Y = 73.409 - 1.361\ X + 0.008\ X^2$
5 Apr. 1979	109	97.15	$Y = 59.722 - 1.234\ X + 0.008\ X^2$
20 Apr. 1979	84	80.36	$Y = 234.333 - 4.095\ X - 0.020\ X^2$
14 May 1979	110	84.32	$Y = 68.022 - 1.327\ X + 0.008\ X^2$
6 June 1979	56	92.71	$Y = -69.449 + 0.843\ X$
21 June 1979	49	70.44	$Y = -34.932 + 0.539\ X$
5 July 1979	24	91.41	$Y = 137.564 - 2.44\ X + 0.013\ X^2$
19 July 1979	20	60.11	$Y = -48.541 + 0.663\ X$
22 Aug. 1979	70	80.01	$Y = 186.455 - 3.150\ X + 0.015\ X^2$
22 Sept. 1979	82	68.32	$Y = -38.548 + 0.584\ X$
2 Oct. 1979	79	95.62	$Y = 71.630 + 1.233\ X + 0.007\ X^2$
16 Oct. 1979	53	88.69	$Y = -44.643 + 0.631\ X$
3 Nov. 1979	89	93.90	$Y = -37.481 + 0.578\ X$
15 Nov. 1979	65	95.70	$Y = 4.819 - 0.237\ X + 0.004\ X^2$
1 Dec. 1979	37	68.44	$Y = -30.428 + 0.508\ X$
14 Dec. 1979	82	96.32	$Y = -43.178 + 0.609\ X$
3 Jan. 1980	96	95.34	$Y = 35.286 - 0.762\ X + 0.006\ X^2$
16 Jan. 1980	86	97.36	$Y = 35.576 - 0.795\ X + 0.006\ X^2$
4 Feb. 1980	93	97.57	$Y = 20.722 - 0.526\ X + 0.005\ X^2$
15 Feb. 1980	79	96.23	$Y = 20.382 - 0.506\ X + 0.005\ X^2$
5 Mar. 1980	80	83.65	$Y = -38.256 + 0.565\ X$
19 Mar. 1980	64	79.38	$Y = -49.710 + 0.662\ X$

Discussion

Both time-specific and cohort-specific estimates indicate that the total annual mortality rate of *S. caprinus* is about 83-99%, depending on postspawning survival. Lower values in this range agree with theory (Royce 1972:238) that total annual mortality is 78-84% if the maximum age is 2.5-3 yr as observed. Higher values are consistent with theoretical annual rates of 90-100% given the 1-2 yr lifespan observed for some year classes.

Variation in postspawning survival might not be due to somatic weight changes because of the lack of a regular monthly pattern and the wide variation in regression elevations between adjacent months, although our somatic weight regressions are based primarily on the 1978 and 1979 year classes which did not disappear after spawning.

TOTAL WEIGHT-TOTAL LENGTH, GIRTH-TOTAL LENGTH, AND LENGTH-LENGTH RELATIONSHIPS

Regression and related analyses for total weight-total length, girth-total length, and length-length relationships are presented in Table 5.

Total length-total weight regressions for adult males and females were not significantly different in slope ($F = 0.029$, df $= 1,657$, $\alpha = 0.05$) or in adjusted means ($F = 1.63$, df $= 1,658$, $\alpha = 0.05$) so that one pooled regression equation was presented for them. Calculated slopes varied significantly from $\beta = 3.0$ ($t = 13.2$, df $= 1,682$, $\alpha = 0.05$) except when data for immatures, males, and females were pooled ($t = 0.197$, df $= 2,792$, $\alpha = 0.05$).

GENERAL DISCUSSION

Stenotomus caprinus, which inhabits the warm temperate Gulf, exhibits markedly different population dynamics from *Stenotomus chrysops*, which primarily inhabits the cold temperate Atlantic north of Cape Hatteras, N.C. Our data and the literature agree that for *S. caprinus*: 1) spawning occurs in one discrete period a year with peak spawning in February or March; 2) all individuals reach maturity and spawn at 90-125 mm TL as they approach age I; 3) maximum size typically is about 200 mm TL, but most fish are much smaller; 4) maximum lifespan is 2.5-3 yr; 5) total annual mortality rate is 83-99%, but postspawning survival, total annual mortality rates, and lifespan vary between year classes; and 6) average sizes are 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. In contrast, *S. chrysops* north of Cape Hatteras 1)

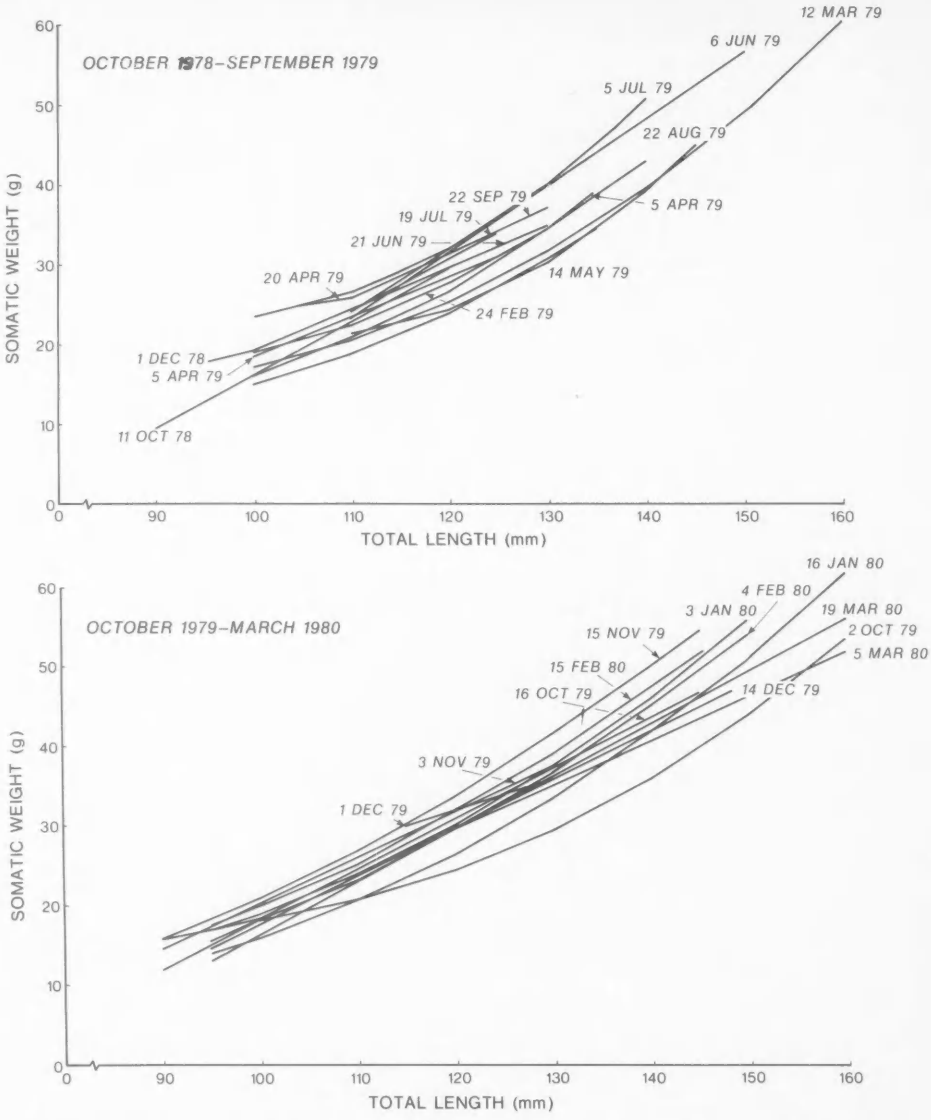


FIGURE 12.—Monthly somatic weight-total length regressions for *Stenotomus caprinus*. The length of each line shows the observed size range.

spawns in the period May-August with peak spawning in June (Bigelow and Schroeder 1953; Finkelstein 1969a); 2) reaches maturity at age II at 182-213 mm TL (Finkelstein 1969a, b; Hamer footnote 9); 3) reaches a maximum size of approximately 480 mm TL (Hamer footnote 9); 4) has a maximum lifespan of 15 yr (Finkelstein 1969a); 5) apparently has a much lower total an-

TABLE 5.—Analyses of total length-total weight (A), length-length (B), and total length-girth (B) relationships for *Stenotomus caprinus*. Lengths and girths are in millimeters and weights are in grams. All regressions were significant at $\alpha = 0.05$. See Methods and Materials for symbols.

Relation	Equation	n	100 r^2	Residual mean square	Corrected total SS for both variables	Means of variables	Observed TL range (not transformed)
A. All fish	$\text{Log}_{10}TW = -4.85 + 3.05\ \text{Log}_{10}TL$	2,793	99.32	0.0017	Log TW = 705.12 Log TL = 75.17	Log TW = 1.28 Log TL = 2.01	21-182
Adult fish	$\text{Log}_{10}TW = -4.13 + 2.71\ \text{Log}_{10}TL$	1,683	90.51	0.0010	Log TW = 18.27 Log TL = 2.25	Log TW = 1.50 Log TL = 2.08	91-182

Relation	Equation	n	100 r^2	Residual mean square	Corrected total SS for dependent variable	Mean of dependent variable	Observed range for dependent variable (not transformed)
B. SL-TL	SL = 0.41 + 0.76 TL	2,776	99.26	3.55	1,326,361.42	81.88	21-182
TL-SL	TL = 0.26 + 1.31 SL	2,776	99.26	6.10	2,280,443.91	116.86	21-182
SL-FL	SL = 0.85 + 0.11 FL	2,421	97.12	4.01	337,068.73	81.88	26-182
FL-SL	FL = 2.90 + 1.14 SL	2,421	97.12	5.40	453,813.15	104.88	26-182
FL-TL	FL = 1.99 + 0.88 TL	2,402	97.36	4.98	452,549.20	104.88	26-182
TL-FL	TL = 0.93 + 1.11 FL	2,402	97.36	6.24	567,821.45	116.86	26-182
TL-G	TL = 8.27 + 0.94 G	2,792	98.00	16.32	2,286,249.29	107.26	21-182
G-TL	G = −6.54 + 1.04 TL	2,792	98.00	18.17	2,545,019.98	105.50	21-182

nual mortality rate, theoretically 26% based on a 15-yr lifespan (Royce 1972:238); and 6) averages 120-155 mm TL at age I, 183-213 mm at age II, and 232-257 mm at age III (Finkelstein 1969a; Hamer footnote 9).

The basic pattern of population dynamics characteristics enumerated for *S. caprinus* is similar to that reported from the Gulf for *Micropogonias undulatus* (White and Chittenden 1977), *Cynoscion nothus* (DeVries and Chittenden 1982), *C. arenarius* (Shlossman and Chittenden 1981), and *Peprilus burti* (Murphy 1981). These findings give additional support to the suggestions (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the Gulf have evolved a common pattern of population dynamics that stresses small size, short lifespan, high mortality rates, and rapid turnover of biomass, especially when compared with congeners or conspecifics north of Cape Hatteras.

The intrageneric variation in *Stenotomus* supports the suggestion of White and Chittenden (1977) that zoogeographic variation in life histories and population dynamics occurs at Cape Hatteras. Unfortunately, the meager information published from the Atlantic coast south of Cape Hatteras does not permit enumeration of population dynamics of *Stenotomus* from that area. However, our findings on *Stenotomus* are consistent with the intrageneric variation in population dynamics within the genus *Cynoscion* at Cape Hatteras (Shlossman and Chittenden 1981), and are similar to the zoogeographic variation reported for *M. undulatus* (White and Chittenden 1977). This zoogeographic variation in population dynamics characteristics has important management implications, because Carolinean Province fish should be less sensitive to growth overfishing than their congeners or conspecifics north of Cape Hatteras.

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VERTICAL MIGRATION AND ITS EFFECT ON DISPERSAL OF PENAEID SHRIMP LARVAE IN THE GULF OF CARPENTARIA, AUSTRALIA

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ABSTRACT

Penaeid shrimp larvae in the Gulf of Carpentaria, Australia, sampled over discrete depths and time intervals showed a day-night pattern of vertical distribution. The magnitude of the migrations increased with larval development. The patterns of vertical distribution were variable and depended strongly on light penetration. Vertical migratory behavior of larvae was linked to currents at various depths. Daily and fortnightly extrapolations of larval displacement showed that vertical migration generally enhanced horizontal advection but the distances and directions were dependent on the current regime and the vertical distribution pattern. It was estimated that larvae could be advected from 70 to 100 km, far enough to traverse the distance from the known spawning grounds to estuarine nursery grounds. Results of this short-term study indicate that differential advection on a seasonal scale may be responsible for the temporal and spatial recruitment patterns of postlarvae observed in the Gulf of Carpentaria.

Vertical migration is widespread among marine and freshwater Crustacea (Russell 1925; Bainbridge 1961). The migration is often periodic and can vary from diurnal and tidal through to seasonal and ontogenetic periodicity. Almost as diverse as the organisms involved are the probable environmental cues that elicit the response and adaptive advantages attributed to this behavior (Bainbridge 1961; Enright 1977; Pearre 1979). Undoubtedly animals have adopted vertical migratory behavior for a variety of immediate and long-term biological advantages (Vinogradov 1968).

Most of the adaptive advantages of vertical migration that have been suggested usually apply to animals that live in relatively deep water with temperature, pressure, light, food, and predator abundance gradients. Shallow-water holoplanktonic and meroplanktonic animals also undergo vertical migrations, however. Because the vertically migrating animal is exposed to different current regimes at different depths (Hardy 1936, 1953), the behavior has been invoked to aid maintenance of position within estuaries (Bousfield 1955; Graham 1972; Weinstein et al. 1980; Wooldridge and Erasmus 1980) and on continental shelves (Walford 1938). It has also been suggested that timed vertical migration enhances horizontal displacement up an estuary (Carriker 1951; Wood and Hargis 1971; Sandifer 1975; Bigford 1979; Sulkin et al. 1980), alongshore (Longhurst 1968; Efford 1970), or onshore (Woodmansee 1966; Penn 1975; Rimmer and Phillips 1979), often against the prevailing currents. In no instance, however, have these mechanisms been demonstrated by monitoring both the vertical behavior and the in situ current regimes simultaneously.

Dispersal, during the pelagic larval phase, is the most likely mechanism that brings postlarval and juvenile penaeid shrimp into shallow-water coastal and estuarine nursery areas from their offshore spawning grounds (Kirkegaard 1975). Evidence of vertical migration of penaeid larvae, which might enhance the onshore movement, is mixed and inconclusive. In the study by Eldred et al. (1965) the larval vertical distribution patterns were variable between species, but appeared to be consistent in the study by Temple and Fischer (1965). A change in behavior from photopositive to photonegative with development was reported by Racek (1959), while a gradual increase in vertical migratory ability, without a phase change, has been seen in other studies (Temple and Fischer 1965; Jones et al. 1970). Most noticeable have been the variable patterns in vertical distribution with varying environmental conditions in studies with repeated sampling (Temple and Fischer 1965; Jones et al. 1970). Nevertheless, based on an idealized larval

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behavior and limited knowledge of current regimes, Penn (1975) hypothesized that larvae of *Penaeus latisulcatus*, off Western Australia, were capable of moving onshore against prevailing currents during certain times of the year.

In this study I attempted to test Penn's (1975) hypothesis by intensively sampling the changes in vertical distribution of penaeid larvae while simultaneously monitoring currents and other environmental parameters in the water column. I hoped to gain insight into the following: the ontogeny of vertical migratory behavior, the environmental factors that control the larval behavior, the current regimes and how they change with depth, and the advective consequences to the larvae resulting from vertical migration through this variable current field.

Staples (1979), studying the postlarvae of *Penaeus merguiensis* in the Gulf of Carpentaria, found discrete temporal and spatial patterns of postlarval recruitment into the rivers around the gulf. These patterns could not be explained entirely by the distribution of adults and the timing of spawning. He proposed that the temporal and spatial patterns of recruitment were caused by the different fates of larvae arising from two peaks of spawning (spring and autumn). While seasonal changes in the direction of larval advection were suggested, little was known about current regimes in the gulf (Cresswell 1971) and nothing known about how these currents would affect the distance and direction of penaeid larval dispersal. This study was, therefore, intended to provide insight into the mechanisms and pathways of larval dispersal and to help explain the variable timing and magnitude of postlarval recruitment.

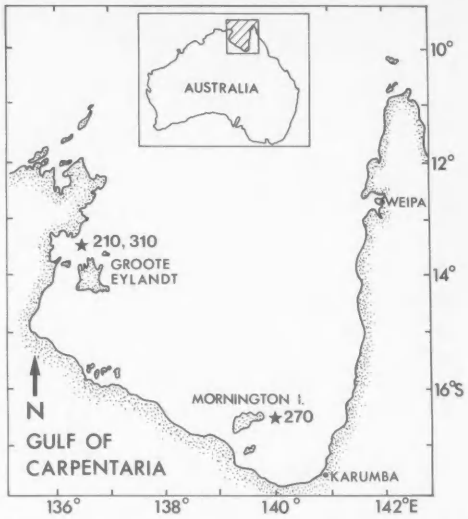

FIGURE 1.—Station numbers and locations for discrete depth sampling (stars) in the Gulf of Carpentaria, Australia.

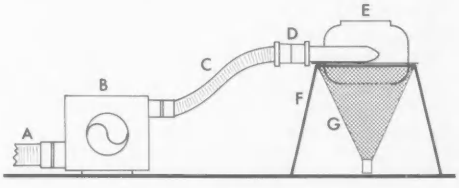

FIGURE 2.—Schematic of pump, water discharge, and filtering system: A) 10.2 cm (4 in) intake hose; B) 7.6 cm (3 in) self-priming centrifugal pump with 6 kW (8 hp) gasoline engine; C) 7.6 cm (3 in) outlet hose; D) quick coupling; E) spinner drum; F) tripod; G) 142 μm mesh plankton net.

MATERIALS AND METHODS

Discrete depth sampling was conducted repeatedly at two locations (Fig. 1) during survey cruises in the Gulf of Carpentaria (Rothlisberg and Jackson 1982). These locations were <30 m in depth and close to known concentrations of adult penaeid shrimp. The ship was anchored on station and a 7.6 cm (3 in) centrifugal pump (Fig. 2), driven by a 6 kW (8 hp) aircooled gasoline engine, was used to pump water from depth. The end of the 10.2 cm (4 in) intake hose was clamped to a weighted wire fed through a meter block. The full length of the hose, in 9.2 m (30 ft) quick coupled lengths, was deployed, regardless of the sampling depth, to prevent variable friction effects. Water from the pump was discharged through a 7.6 cm (3 in) diameter hose tangentially into a drum (spinner) mounted on a tripod. Upon loss of velocity the water drained gently through a 56 cm diameter plankton net (142 μm mesh) suspended beneath the spinner. The outlet hose was coupled to the spinner in such a manner that it could be inserted and withdrawn quickly to allow precisely timed pumping intervals. The pumping rate (up to 1,000 l/min) was monitored with timed fills of a container of known volume.

The water column was divided into four strata, and the inlet placed at the center of the stratum. The pump was brought to speed, the outlet hose inserted in the spinner, and the stratum sampled

for a 15-min interval. After 15 min the outlet hose was quickly withdrawn, the pump speed reduced, and the hose inlet lowered to the next stratum for 5 min of flushing before the next 15-min sample was taken. The four strata were therefore sampled in a 75-min pumping series which was initiated every 2 h and continued for 24-36 h.

At the same time that the pump inlet was being deployed astern on the main wire, a Lerici current meter (Frassetto 1967), modified for deck readout of current velocity, was deployed amidship on the hydrographic wire. Fifteen-minute records at each depth stratum were obtained simultaneously with plankton samples. All current meter records were annotated on a strip chart recorder in the deck readout unit.

To link the vertical distribution of the shrimp larvae to the current vectors at depth, the median level of larval vertical distribution was calculated (Cronin and Forward 1979) for each of the larval substages at each 4-h time interval and assigned to one of the four depth strata. The intermediate (2-h) larval distributions were interpolated from the 4-h time series. The current vectors for each 2-h time interval, associated with the depth stratum (levels 1-4) to which the median larval depth corresponded, were added progressively over 24 h for each larval substage (Fig. 7b, c). In addition to the median larva, three other hypothetical behavior patterns were modelled: 1) a nonmigratory surface dwelling animal; 2) a nonmigratory near-bottom dwelling animal; and 3) a larva (12:12 larva, Figs. 7, 8, 9) that followed the behavior pattern dictated by Penn's (1975) hypothesis, i.e., it moved the full height of the water column on a strict 12:12 day: night cycle for the entire length of the larval life.

A photometer, with both deck and submersible cells, was used to measure the ambient and submarine irradiance ($\mu W/cm^2$). Irradiance levels were recorded at 2 m intervals at the start of every 2-h pumping series during daylight. The meter was not sensitive enough to record variable levels of moonlight or starlight. Temperature profiles were obtained with both a bathythermograph and water sampled from the pump outlet.

Plankton biomass (settled volume) from discrete depth samples was obtained by settling the fixed sample (10% formaldehyde, sodium tetraborate buffer) for 4 h in Imhoff cones (Rothlisberg and Jackson 1982). The samples were then transferred to 2% 2-phenoxy ethanol for preservation and subsequent microscopic examination. For economy and expediency, only every other sampling series (4-h) was examined. No subsampling scheme was employed. Numbers of larvae in each sample were standardized to numbers per cubic meter based on the calibrated pumping rates.

RESULTS

Ontogeny of Vertical Migration

From sampling done on 22 and 23 March 1977 north of Groote Eylandt (Station 210), early larvae (zoeal stages 1-3) were seen to move up into the water column only at night (Fig. 3). This movement was very limited and rarely extended more than one-half the distance to the surface. By day they were almost totally restricted to the bottom stratum of the water column sampled. The mysis stages extended the range of their nighttime excursions to the full water column without completely abandoning the lower part of the water column at night. They too returned almost completely to the bottom stratum by day. Postlarval numbers in the samples were too few to make generalizations, but they did appear to

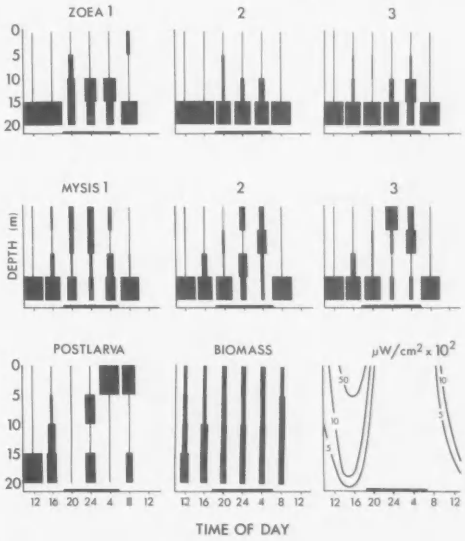

FIGURE 3.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance ($\mu W/cm^2$) for 22-23 March 1977 at Station 210 north of Groote Eylandt. The dark horizontal bar indicates night.

extend the mysis pattern further by almost completely abandoning the lower parts of the water column by night but still returning by day.

Variations in the Pattern of Vertical Distribution

High light penetration was characteristic of the station occupied on 22 and 23 March 1977 (Fig. 3). Conditions were calm, isothermal, and clear with a secchi disc depth of 16 m in the 22 m water column and penetration of the 1,000 μW/cm^2 isolume to 20 m. Under these conditions, movement of the larvae away from the deepest stratum occurred only at night and almost all stages (first zoea (Z1) through third mysis (M3)) returned to the bottom stratum during daylight.

On 6 and 7 May 1977 (Station 310), though sea state and wind conditions were comparable with the previous sampling session, increased turbidity limited the 1,000 μW/cm^2 isolume penetration to only 10 m or about half of the water column (Fig. 4). This change in light penetration paralleled marked changes in the vertical distribution of all larval stages. During daylight, early larval stages (zoea 1-3) were not confined to the bottom stratum. The day-night differences in vertical distribution, though present, were less distinct than in the previous case, and these early larval stages were seen even at the surface at night. The day-night pattern for mysis stage larvae was even less distinct. Though spread throughout the water column, they appeared to be slightly more concentrated at or near the surface at night. Postlarval (PL) numbers were again low, and they were near the surface during the entire diel period. They were more abundant in the surface stratum during the night.

At the station east of Mornington Island on 27 and 28 March 1977 (Station 270) the wind and sea conditions were extremely calm but light penetration was even more diminished than in the previous two cases. On this occasion the 1,000 μW/cm^2 isolume penetrated only about one-third of the water column (Fig. 5). Further changes in the patterns of larval distribution were seen. Early larval stages were concentrated in the middle two depth strata with nighttime movements to the surface. The mysis stage larvae were also predominantly in the middle part of

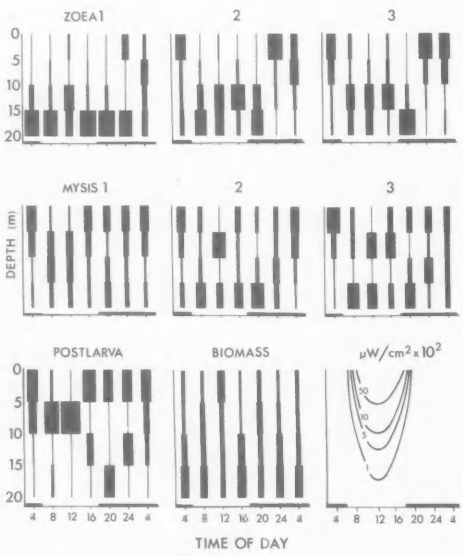

FIGURE 4.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance (μW/cm^2) for 6-7 May 1977 at Station 310 north of Groote Eylandt. The dark horizontal bar indicates night.

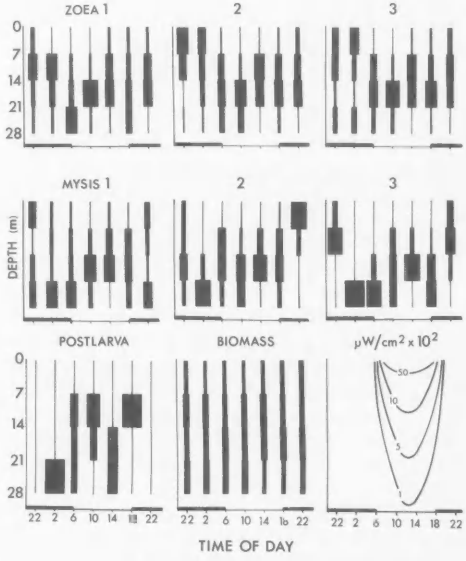

FIGURE 5.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance (μW/cm^2) for 27-28 March 1977 at Station 270 east of Mornington Island. The dark horizontal bar indicates night.

the water column by day but spread out to both the surface and the bottom strata at night. Again the postlarval numbers were low and little day-night patterning was evident. No postlarvae were caught at any time in the surface stratum and were near the bottom both day and night.

Of concern was possible day-night variation in larval abundance due to avoidance of the inlet hose and/or larval distribution outside the range of the sampler. Of particular concern was the possibility that during the day larvae were on or near the bottom below the hose inlet at its lowest extent. To test statistically for a temporal variation in larval abundance, the larval numbers were initially combined over all depths within a sampling time interval and then a square root transformation was applied. A sine curve was fitted to estimate gradual rather than abrupt day-night changes in larval numbers. Postlarval numbers were too low to include in the analysis. Time alone was highly significant for the total number of larvae and significant at lower levels for three of six larval substages (Table 1). The high level of significance of the station-time interaction for all but the Z2 larvae indicates that the small diel variation in abundance was variable between sampling occasions. Inspection of the data showed that the peak abundances varied by stage, location, and time of day and that there was no systematic difference in catchability which would bias the interpretation of the diurnal patterns shown previously.

To add confidence to the diagrammatic interpretation (Figs. 3-5), further analysis, using an arc-sine transformation of the proportional larval abundances by depth also, showed that the abundances at the four depth strata were quite variable from one date to the next. This was indicated by the high degree of significance of the station effects at almost all depths (Table 2). The abundances of larvae in the surface stratum (level 1) showed the most consistent relationship with time of day, with larvae rarely at the surface by day, on any cruise, and increasing in abundance at the surface by night. Further, the station-time interaction at depth (e.g., level 3) was significant for most larval stages and substages, indicating a high degree of station-to-station variation in the depth of peak abundance.

TABLE 1.—Summary of analysis of variance of larval abundance. A square root transformation was applied to all data pooled within each time increment over all four depths.

Stage/ substage	F-ratios: Station (2, 11 df)	Time (2, 11 df)	Station-time interaction (4, 11 df)	Error mean square
Zoea	9.98**	4.92*	4.89*	2.6519
Mysis	32.04***	3.58+	4.82*	1.6531
Total	56.63***	18.03***	10.75***	1.0528
Z1	6.21*	1.98	6.31**	0.8505
Z2	11.86**	4.86*	2.89+	1.4859
Z3	11.49**	4.81*	8.33**	1.0520
M1	33.30***	2.94+	3.49*	1.8837
M2	25.72***	1.66	13.65***	0.2452
M3	40.68***	0.13	12.88***	0.2976

***$P<0.001$, **$P<0.01$, *$P<0.05$, + $0.05<P<0.10$.

TABLE 2.—Summary of analysis of variance of proportional larval abundance at four discrete depths. An arc-sine transformation was applied to the percentages.

Stage/ sub-stage	Level	F-ratios: Station (2, 11 df)	Time (2, 11 df)	Station-time interaction (4, 11 df)	Error mean square
Zoea	1	7.53**	5.29*	2.56+	0.03293
	2	17.01***	0.72	2.15	0.02167
	3	4.56*	0.60	6.49**	0.02906
	4	22.68***	2.31	2.10	0.04125
Mysis	1	7.33*	16.11***	0.76	0.02179
	2	10.55**	1.94	8.46**	0.01277
	3	7.68**	2.58	3.35+	0.01925
	4	14.89***	1.25	9.27**	0.03075
Z1	1	1.25	0.13	2.10	0.03876
	2	10.61**	0.78	0.91	0.04839
	3	3.84+	0.59	7.31**	0.03953
	4	12.74**	2.12	3.27+	0.05937
Z2	1	6.65*	7.42**	2.23	0.04838
	2	17.53**	0.46	1.59	0.02760
	3	8.85**	1.03	5.56*	0.03270
	4	30.46***	3.48+	0.97	0.05877
Z3	1	11.05**	6.43*	2.38	0.3573
	2	9.99**	0.27	1.09	0.03112
	3	4.03*	1.89	4.10*	0.04522
	4	14.00***	0.47	1.22	0.09720
M1	1	9.13**	16.15**	0.35	0.01989
	2	13.82***	0.27	5.78**	0.01714
	3	4.26*	1.90	3.39*	0.02365
	4	40.92***	2.24	21.86***	0.01289
M2	1	2.50	4.97*	1.11	0.06961
	2	2.06	0.34	1.07	0.08163
	3	3.31+	0.20	3.02+	0.05118
	4	5.70*	1.06	2.44	0.10437
M3	1	4.85*	9.31**	0.80	0.05065
	2	1.21	0.16	2.27	0.09051
	3	3.74+	1.01	9.24**	0.03211
	4	2.22	1.51	2.13	0.16646

***$P<0.001$, **$P<0.01$, *$P<0.05$, + $0.05<P<0.10$.

Consequences of Vertical Migration

At the two sampling locations in the Gulf of Carpentaria, the currents were dominated by a tidal component as seen in the individual current vectors, represented by the mean speed and direction for the 15-min sampling periods (Fig. 6). Detailed analyses of these records, however, were complicated by three factors: 1) time lag between sampling surface and bottom strata; 2) short-term wind events; and 3) anomalous current vectors at depth. At most sampling times,

current speed and direction changed with depth. Although the speed usually decreased with depth (e.g., Fig. 6a, 0200; 6c, 2200), an increase was noted on some occasions, especially around the time of slack water (e.g., Fig. 6a, 1200; 6b, 0000). This apparent increase is believed to be an artifact of the time lag in sampling with the migrating current meter. Short-term wind events can also be detected at the surface stratum (Fig. 6b, 2.5 m; 1800-2200). Time lag and wind events alone, however, cannot explain all the variation in the current vectors. Other anomalous current vectors at depth (e.g., Fig. 6a, 1000, 17.5 m; 0800, 7.5 m) represent short-term nontidal perturbations of unknown origin.

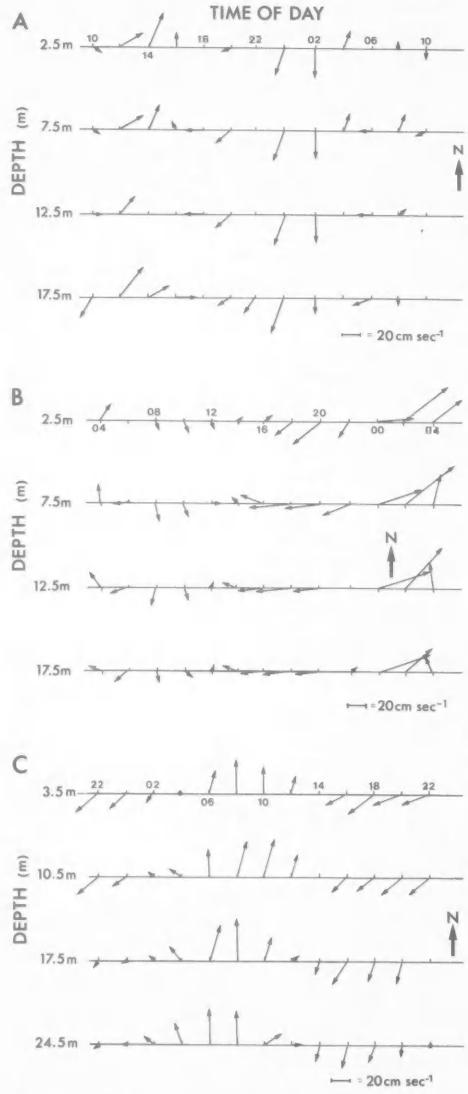

FIGURE 6.—Mean 2-h current vectors at four depths and three stations: A) Station 210, 22-23 March 1977 north of Groote Eylandt; B) Station 310, 6-7 May 1977 north of Groote Eylandt; C) Station 270, 27-28 March 1977 east of Mornington Island.

Over the 24-h sampling period at Station 210, the net displacement (measured as a straight line from the origin to the end of the progressive vector) was quite variable for migratory and nonmigratory animals. Surface-dwelling animals would have been displaced to the northwest, near-bottom dwelling ones to the south, and the 12:12 larva almost due west. The net drift of the 12:12 larva was considerably less than either of the nonmigratory animals. The larval movements (Fig. 7b, c) based on sampled vertical distributions would have closely paralleled the bottom currents in this case because so much of their time was spent in the lower parts of the water column. The slight differences in displacement direction and distance between substages reflect the differences in depth distribution. Because of their wider excursions, the postlarvae were exposed to more of a mixture of the bottom and surface currents and therefore approached the 12:12 larva in direction of advection during that larval stage. To calculate an approximate total displacement over the whole of the larval phase, the 24-h picture was extrapolated by making several assumptions. Firstly, the larval life span was set at 14 d with 2 d for each larval substage (Z1, Z2, Z3, M1, M2, M3, PL). Secondly, within each substage the same vertical migratory behavior prevailed on both days. Thirdly, the current regime, seen during the 24-h sampling period, was constant over the 14-d larval life. By doubling the length of the daily resultant vectors for each larval substage and adding them progressively, the 2-wk displacement is approximated (Fig. 7d). The calculation of absolute distances is not precise because of the nature of the assumptions, especially the third. The period of sampling was, however, between neap and spring tides so the tidal currents would have been moderate and a reasonable approximation of mean velocities over the tidal cycle. Under these criteria, the median larva would have been displaced about 69 km (37 nmi), the 12:12 larva 25 km (13 nmi),

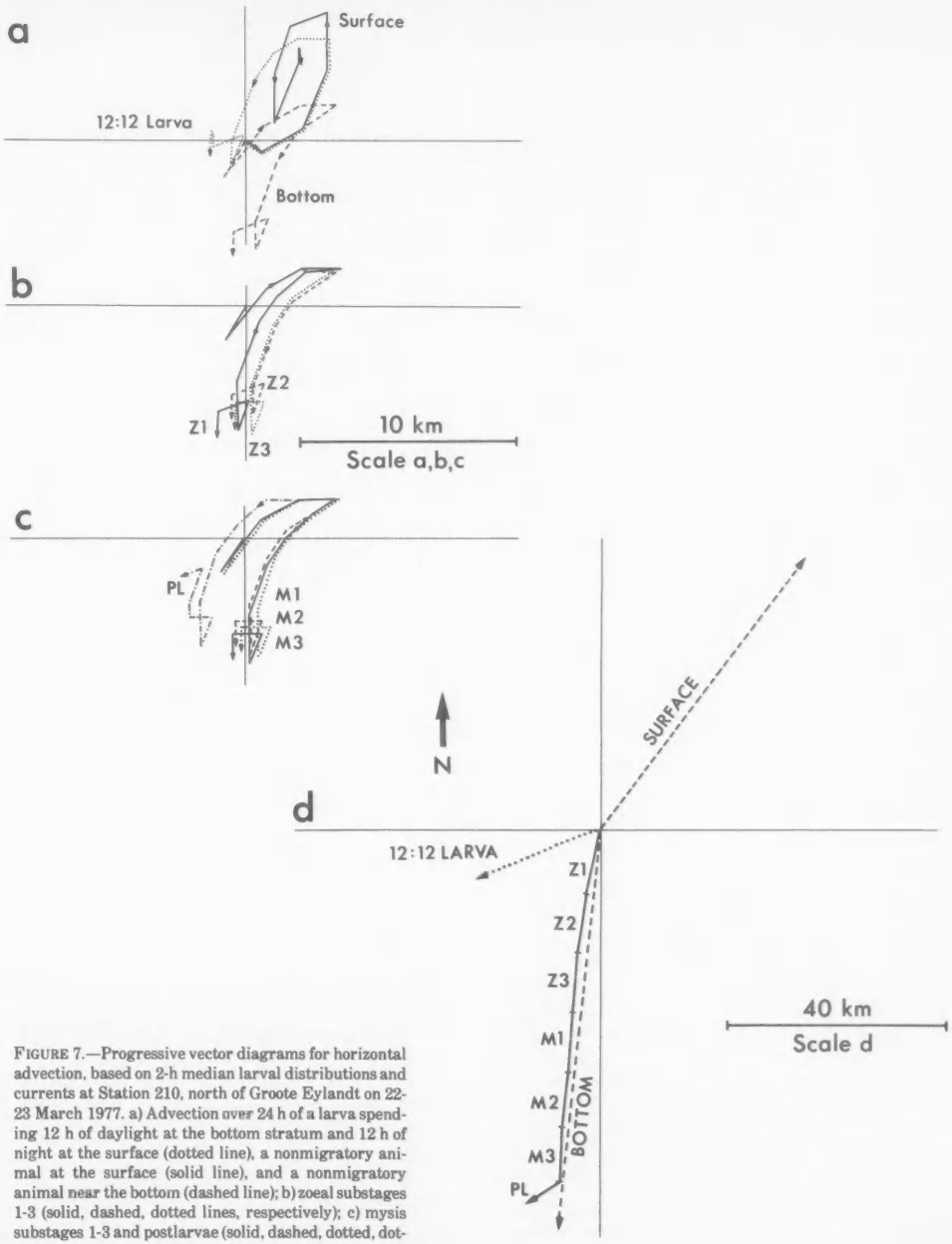

FIGURE 7.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 210, north of Groote Eylandt on 22-23 March 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

and the surface and near bottom nonmigratory animals 62 km (34 nmi) and 72 km (39 nmi), respectively. The larvae were displaced to the southwest from the sampling station north of Groote Eylandt. This trajectory would have taken them in the general direction of Groote Eylandt or the coastal rivers in the Limmen Bight, southwest of Groote Eylandt. Greater distances could be attained if the pelagic postlarval stage was maintained through several instars before metamorphosing to the benthic-living juvenile shrimp.

Procedures for approximating displacement distance and direction on the other two sampling occasions were similar but the resultant displacements were quite different because of the different vertical distribution patterns seen on each occasion. At Station 310, north of Groote Eylandt, submarine irradiance was reduced and the vertical distribution of the larval substages was more varied (Fig. 4). Consequently, the horizontal displacements of individual larval substages (Fig. 8b, c), though dominated by the bottom currents (Fig. 6b), were quite varied. The hypothetical 2-wk displacement was again in the same direction as the bottom current (Fig. 8d), but the distance was enhanced by the fact that larvae were further off the bottom in their nightly excursions for slightly higher proportions of the time. Total horizontal displacement over the 2-wk larval period, up to and including 2 d of postlarval life, would be about 75 km (40 nmi). The direction of advection of the median larva in this case is to the northwest. The 12:12 larva would have been displaced seawards to the central Gulf of Carpentaria.

Analysis of the larval migratory patterns (Fig. 5) and the current regime (Fig. 6c) at Station 270 east of Mornington Island showed yet another pattern of displacement (Fig. 9). Here, because there were large numbers of larvae in the upper part of the water column both night and day, the displacement would have been in the direction of the surface currents (Fig. 9a, b, c). Slight deflection away from the surface direction was seen in older larvae (M1-PL) as more of them moved into the lower part of the water column (Fig. 9d). The displacement distance over the 2-wk period would have been 98 km (53 nmi). All advection was to the west, with the 12:12 larva going to the southwest towards the coast and the median larva heading west-northwest, away from the coast, in the general direction of the surface currents.

DISCUSSION

While it is widely thought that changes in light intensity are the primary environmental cues that initiate and control the diel vertical migrations in aquatic animals (Ringelberg 1964; Thorson 1964; Boden and Kampa 1967; Hutchinson 1967; Segal 1970; Buchanan and Haney 1980), there have been cases in which the timing of the migration was not strictly in phase with changes in light intensity, possibly because of changes in subsurface light and/or feeding history and strategy of the animals (Enright and Honegger 1977; Bohrer 1980). In shallow-water coastal environments, factors affecting light penetration and therefore vertical distribution of animals are numerous and subject to rapid change. Turbulence with concomitant turbidity caused by both wind and tidally induced currents, river and coastal runoff, and rapid phytoplankton growth would be the more significant causes of light reduction. It is these short-term changes in submarine irradiance that are probably responsible for some of the conflicting reports about whether or not penaeid larvae migrate vertically.

The first mention of differential vertical distribution of penaeid larvae is by Racek (1959), sampling off the eastern Australian coast. His sampling was not strictly stratified, he published no supportive data, and the conclusions are probably drawn from a combination of field and laboratory observations. He stated that nauplii as well as first and second protozoeae (= zoeae) were strongly attracted to bright light. I saw no evidence of this in our field collections but have observed it under artificially high light intensities in the laboratory. There may be some threshold light intensity at which point penaeid larvae shift their behavior from photonegative to photopositive similar to that described for the larvae of *Uca pugilator* (Herrnkind 1968). From his field sampling, Racek found that late protozoeae and early mysis stages rose to the surface at night and sunk to lower strata during daylight. The vertical distribution of late mysis and postlarvae were not mentioned in Racek's brief account.

In the study by Eldred et al. (1965), the day-night pattern of vertical distribution was neither persistent within nor consistent among genera. For *Penaeus duorarum* only postlarvae were discussed. Pooled samples were dealt with, so little information about station-to-station variation

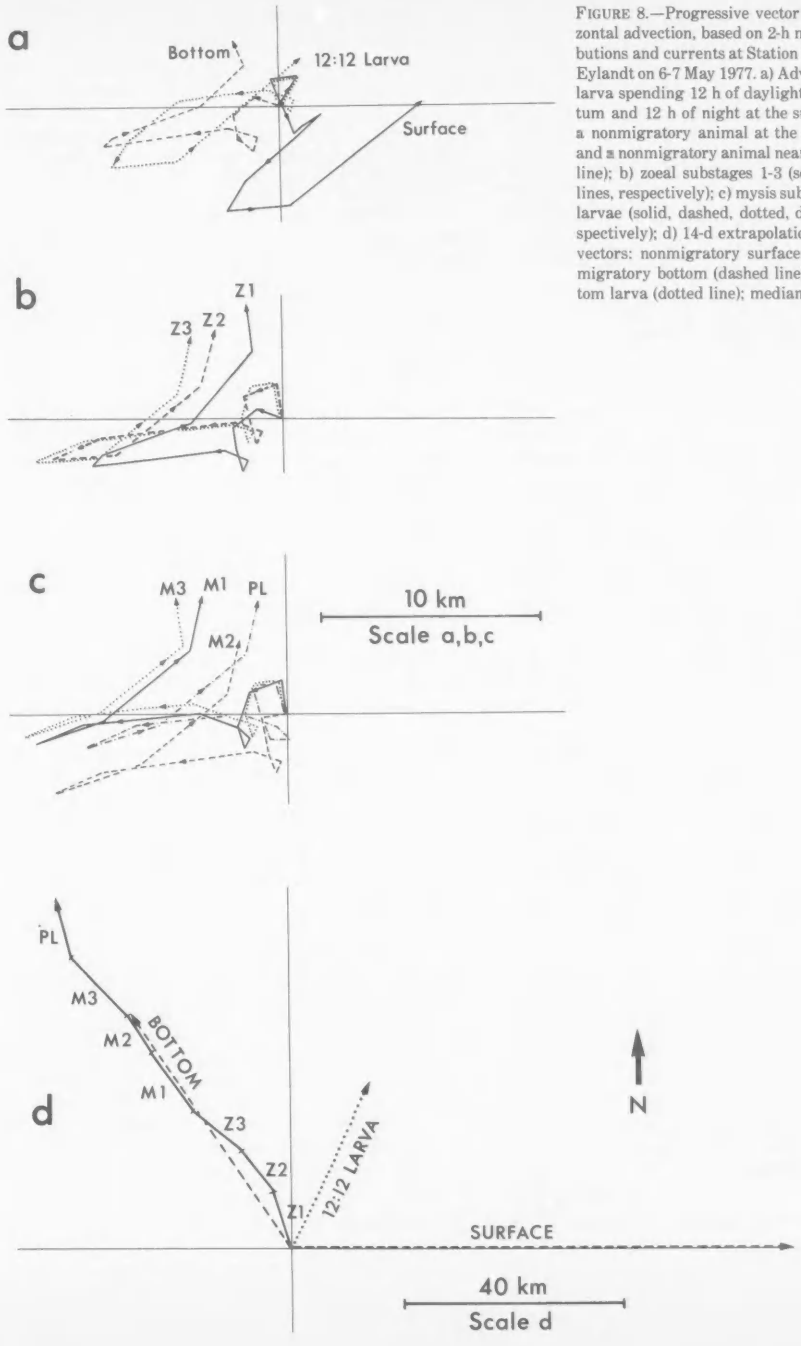

FIGURE 8.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 310, north of Groote Eylandt on 6-7 May 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

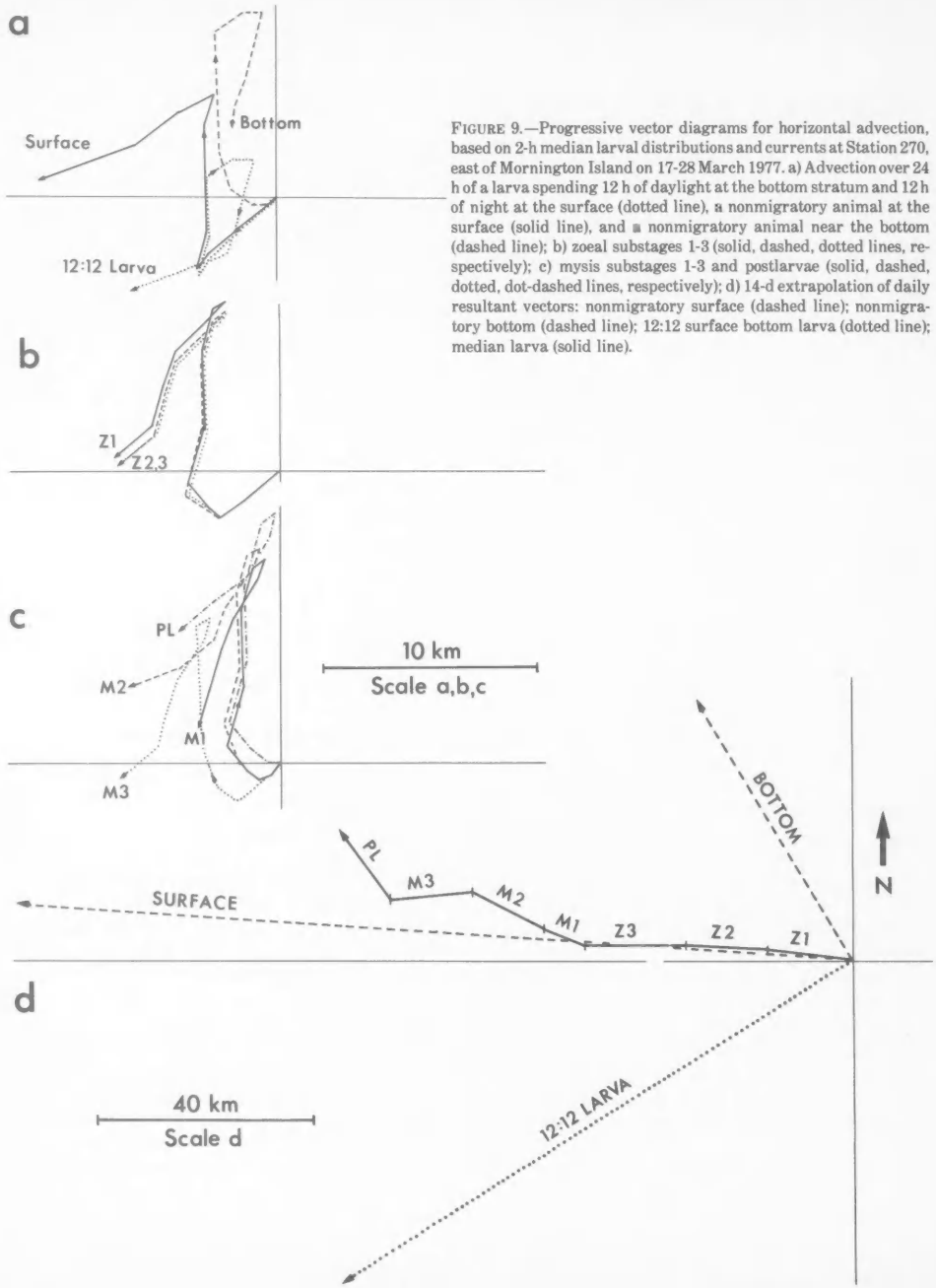

FIGURE 9.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 270, east of Mornington Island on 17-28 March 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

can be obtained. The broad picture based on percentages indicated that more postlarvae occurred at the surface than near the bottom during daylight while more were near the bottom at night. The actual locations were not given but were probably pooled observations of a number of nearshore stations. Thus, the possibility exists that these postlarvae, close to nearshore nursery grounds and sampled mostly on flood tides, were in a tidally induced behavior pattern that has been shown for the postlarvae of *P. duorarum* (Hughes 1969a, b), *P. aztecus* (St. Amant et al. 1966), *P. plebejus* (Young and Carpenter 1977), and *P. merguiensis* (Munro 1975; Staples 1980). The zoeal and mysis-stage larvae of *Trachypenaeus* and *Sicyonia* were also sampled in the Eldred et al. (1965) study. These early larvae (all stages pooled) showed a marked increase in abundance near the bottom during the day and slightly increased abundances at the surface at night. In their summaries, no larval distributions with intermediate depths and times were shown. In the Gulf of Carpentaria there are at least eight genera represented: *Penaeus*, *Metapenaeus*, *Atypopenaeus*, *Parapenaeopsis*, *Trachypenaeus*, *Metapenaeopsis*, *Solenocera*, and *Eusicyonia*. When generic resolution was applied to the present series of samples, no changes in the patterns emerged, but the numbers of larvae available for each analysis decreased. It therefore seemed reasonable to analyze the pooled samples since it appeared the behavioral patterns were family-wide.

Temple and Fischer (1965) were the first to show clear patterns of vertical distribution by penaeid larvae. They too were sampling mixed genera of penaeids (*Penaeus*, *Trachypenaeus*, *Sicyonia*, and *Solenocera*). Using discrete depth sampling nets, they showed some increase in migratory ability with the development of the larval stages, as well as the variable patterns seen on different sampling occasions. They did not measure light penetration and attributed the variations of larval distribution to differing conditions of water column structure and stability, as characterized by the presence or absence of a thermocline. The same degree of variation in vertical migratory patterns was seen in this study under isothermal conditions, in calm to slight seas. Therefore, turbulence seemed to be of minimal importance in explaining the differences in distribution patterns. However, even under near uniform wind and sea conditions, light penetration in the shallow coastal stations was quite variable and this variation was reflected in larval behavior. It therefore appears that light penetration is the dominant environmental variable affecting larval behavior. There is little doubt, under conditions of strong vertical mixing in shallow water, that both turbulence and the concomitant increase in turbidity would result in a mixed vertical distribution. Temple and Fischer (1965) also believed that there was evidence for a reversal of vertical distribution with growth from zoeal to postlarval stage. Their summary figure (fig. 3, p. 62) is not convincing and again may be biased by the change in behavior of postlarvae to a tidally dominated one used to enter coastal estuaries (Temple and Fischer 1965). In the Gulf of Carpentaria sampling, there was no evidence of a reversal with development, but these samples were taken well offshore so a tidal-coastal behavior pattern cued by salinity or pressure differences was probably not in evidence.

Only one other study of larval penaeid vertical migration has been undertaken; Jones et al. (1970) sampled *P. duorarum* larvae off southern Florida. Summary figures of pooled data also show the ontogenetic change in vertical migratory ability of the larvae, as well as variability in the patterns between sampling periods. No environmental data are provided to help explain the difference.

All these studies (Racek 1959; Eldred et al. 1965; Temple and Fischer 1965; Jones et al. 1970) were undertaken to help explain how the vertical distribution of penaeid larvae affects dispersal from offshore spawning grounds to nearshore or estuarine nursery grounds. None of the studies, however, was able to explain the variable results encountered, and furthermore, the currents that would be responsible for this onshore movement were not measured. Penn (1975) attempted to overcome these deficiencies by using an idealized larval behavior, one which required all larvae to move the full height of the water column from the surface to the bottom on a strict night-day cycle (12:12 larva in Figs. 7, 8, 9). This, however, did not allow for differential larval abilities and/or environmentally induced variations in behavior. Furthermore, because of the lack of in situ current recordings, he used differences in predicted tide heights to calculate residual flows. Penn found, even with these constraints, a general mechanism by which larvae could be transported farther inshore at night than offshore during the day, against the prevailing cur-

rents between March and August, the main period of postlarval recruitment in Shark Bay, Western Australia. Penn proposed that during a larval life lasting 2-4 wk the larvae would be displaced 30-80 km before becoming postlarvae at which time they would migrate more actively using a tidal cue. In the present study the 12:12 larva that behaved in a manner dictated by Penn's (1975) scheme seldom travelled in the same direction or distance as the median larva (Figs. 7, 8, 9). This is largely because these larvae did not utilize the full water column over all their larval life even under ideal conditions and that subtle changes in environmental factors changed the patterns of vertical distribution of all larval stages quite markedly.

With more detailed information on larval distribution and its causes, realistic dispersal distances and directions are even more dependent upon detailed knowledge of current speeds and direction at depth. In the present study there were shortcomings in assessing both short-term and long-term in situ current regimes. The migratory current meter used gave some indication of variation of speed and duration of currents but is probably biased by sampling technique and influenced, at times, by short-term wind events and short-term nontidal pertubations. Furthermore there were errors introduced by deploying the meter from a moored vessel. A certain amount of oscillation in current direction appeared during periods of low current velocity when the ship would swing on its anchor. This was overcome to some extent by using both a bow and stern anchor. The most serious shortcoming, however, is the robustness of the extrapolation from the 24-h record to the entire larval life of about 14 d. At best this would only be an approximation of the distance and direction of advection of median larva.

The distances estimated by extrapolation (ca. 70-100 km) are large enough to transport the larvae from the farthest known offshore commercial concentrations of adult penaeid shrimp in the Gulf of Carpentaria (Lucas et al. 1979) to their nearshore and estuarine nursery grounds. This range of advection is greater than that estimated by Penn (1975) even though in this study only a 2-wk larval life was used as opposed to a 4-wk period in his. The 2-wk period seems more realistic at ambient Gulf of Carpentaria temperatures (unpubl. data; Cook and Murphy 1969; Mock and Murphy 1971). This period still allows for one to two postlarval intermolts before settlement. It is suggested that the advection of the larvae limits the offshore adult distribution of those species of penaeid shrimp in the Gulf of Carpentaria that rely on nearshore or estuarine habitats for juvenile nursery grounds. There are no apparent depth or substrate limitations that would restrict the adult distribution to a coastal zone <100 km wide.

Whether or not differential larval advection can account for the large-scale temporal and spatial patterns of postlarval recruitment seen in the Gulf of Carpentaria (Staples 1979) is still open to speculation. There is some evidence from this study of offshore transport of larvae in March (Fig. 9d) at a time when large numbers of ripe female shrimp are present in the commercial fishery in the southeastern corner of the Gulf of Carpentaria. It may be this offshore advection of larvae that explains the subsequent low level of postlarval recruitment in the following weeks into the coastal rivers of this region of the Gulf of Carpentaria (Staples 1980). The short-term sampling of currents in the present study is not capable of annotating the long-term seasonal effects of tropical wind regimes and the long-term progression of tidal phase. Long-term monitoring and modelling of tidal and wind driven currents (Church and Forbes 1981; Forbes and Church in press) in the Gulf of Carpentaria has recently been completed and will be used to overcome this shortcoming of the present study. It is also likely that a better understanding of short-term meteorological events at critical times in the larval life history would help explain the year-to-year variation seen in the strength of postlarval recruitment in individual rivers around the gulf (Staples 1979) and the subsequent commercial catch (Lucas et al. 1979).

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FEEDING ECOLOGY OF 0-AGE FLATFISHES AT A NURSERY GROUND ON THE OREGON COAST

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ABSTRACT

The food habits of 0-age English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*; were investigated over a 2½-year period at a shallow nursery area (9-30 m) off the central Oregon coast. A total of 422 guts from recently metamorphosed fish (17-88 mm SL) were examined; only 16 were empty (4%). The greatest similarity in diets was between English and butter soles. Both species were benthophagous, feeding on a wide variety of prey, including palps of the polychaete *Magelona sacculata*, juvenile bivalves, siphons from tellinid clams, harpacticoid copepods, amphipods, cumaceans, and juvenile decapods. Speckled sanddabs fed equally on benthic prey (amphipods, cumaceans, decapods) and mysids, while sand sole almost exclusively ate mysids. The guts of all four species tended to be <25% full in the morning before 0900 h; stomach fullness gradually increased during the late morning and afternoon.

Food habits of English sole were a function of location of capture within the study area, season, and fish length. Juveniles <35 mm SL fed on small prey, e.g., polychaete palps, juvenile bivalves, tellinid clams, and harpacticoids, while larger individuals fed on larger prey, e.g., amphipods, cumaceans, and decapods. Diets of English sole <35 mm SL varied greatly both between seasons in the same year and between years. Spatially, the diets of English sole captured in trawls at the same depth and different depths were similar in January 1979 but highly variable in May 1979. These temporal and spatial differences in feeding are probably caused by seasonal changes in the abundance and spatial distributions of benthic prey.

Many juvenile flatfishes recruit to the sea floor in well-defined nursery areas following metamorphosis from pelagic larvae. The types and densities of food items present in such benthic regions potentially can affect growth and mortality of recently settled flatfish species (Paloheimo and Dickie 1966; Steele et al. 1970; Cushing and Harris 1973). In addition, whenever the nursery grounds of several species coincide or overlap, interspecific interactions originating from similarities in diet may also be a factor regulating growth and survival (e.g., Edwards and Steele 1968). Four species of pleuronectiform fishes—English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*—utilize the shallow water of the open Oregon coast as a site of benthic recruitment and early growth. All but *C. stigmaeus* are important to the Oregon trawl fishery. English sole ranks among the top three commercial species based on annual landings.

In conjunction with a long-term research program designed to improve management of Oregon's multispecies demersal fishery (Pearcy et al. 1977; Richardson and Pearcy 1977; Pearcy and Hancock 1978; Laroche and Richardson 1979; Hayman and Tyler 1980), we examined the prey selected by recently settled individuals of these four species at one site over a 2½-yr period. Our specific goals were to describe the food habits of these fishes, to relate the temporal and spatial variability of the English sole diet to changes in prey abundance and distributions, and finally to compare the dietary and habitat overlap of English and butter soles.

MATERIALS AND METHODS

The area selected for this work was located off Moolach Beach on the open Oregon coast (Fig. 1). Situated between Yaquina Head and Cape Foulweather 10 km north of the nearest estuary, this site has been the focus of recent work on the recruitment and growth of juvenile pleuronectids (Laroche and Holton 1979; Rosenberg 1981; Krygier and Pearcy[2]) and the food habits of adult

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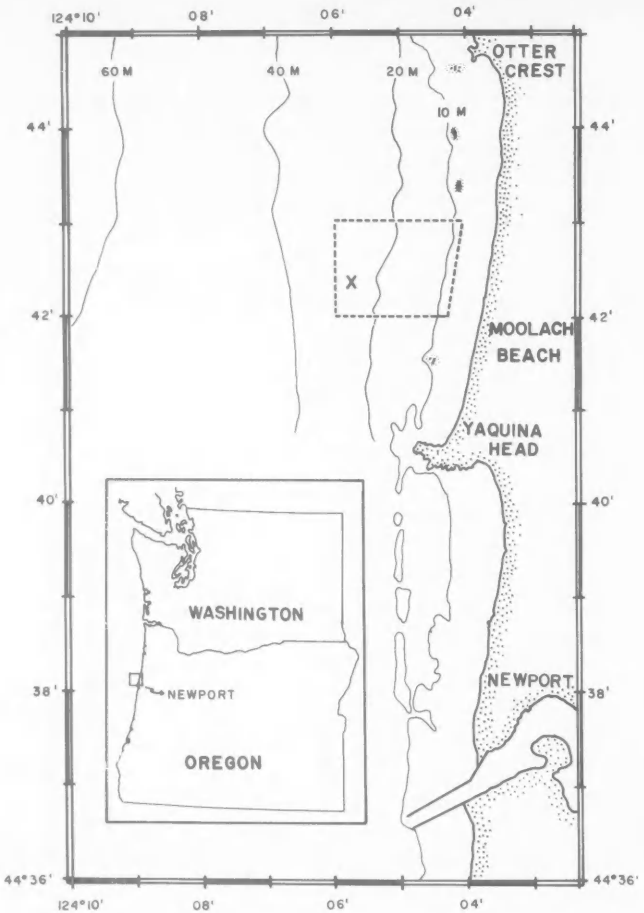

FIGURE 1.—Location of study area. Dotted lines enclose area from which beam trawl samples were collected; "X" marks location of box core and Smith-McIntyre grab samples.

flatfishes (Wakefield[3]). Trawl samples collected from this area between May 1977 and September 1979 were utilized for our work. A 1.5 m beam trawl fitted with a recording odometer wheel and a 7 mm stretch mesh liner was employed for all but one of these collections. On one occasion, 22 March 1979, we obtained samples using a small otter trawl which also had a 7 mm stretch mesh liner. On each sampling date, 10-min tows covering about 750 m^2 surface area were made at several depths between the 9 and 30 m isobaths (0.9 and 2.7 km offshore, respectively). Fish were preserved in 10% buffered Formalin[4] immediately upon collection. No regurgitation of gut contents was observed. The daily time of sampling varied between 0830 and 1800 h.

From the 85 trawl collections obtained during this 29-mo period, we selected 31 for examination. Several criteria were used in choosing these samples. In keeping with an overall goal of the Pleuronectid Project to obtain detailed informa-

Unpubl. manuscr. School of Oceanography, Oregon State University, Corvallis, OR 97331.

[3]W. W. Wakefield. Feeding ecology within an assemblage of benthic fishes on the Oregon Continental Shelf. Unpubl. manuscr. School of Oceanography, Oregon State University, Corvallis, OR 97331.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tion on the most important commercial species, emphasis was placed on those trawls which contained English sole. Priority was also given to using samples which were collected between July 1978 and September 1979, since quantitative meiobenthic samples were also gathered from the study area during that period. We used selected trawl collections from 1977 and 1978 to investigate the between-year repeatability of trends noted in the 1979 data. Finally, only hauls containing specimens 70 mm SL and less were used.

In the laboratory a size range of juvenile flatfish was selected from each of the trawls chosen for study. Standard length of each specimen was recorded prior to removal of the gut. Both the stomach and intestinal tract were removed and opened under a dissecting microscope; gut contents were identified to the lowest possible taxon and counted. We used a subjective scale ranging between 0 and 4 to quantify the degree of gut fullness (0 = <5% full, 1 = 5-25% full, 2 = 25-50% full, 3 = 50-75% full, 4 = 75-100% full).

Quantitative data for each prey category were summarized in two ways. The frequency of prey occurrence, expressing the proportion of all fish sampled which had a given food item in their gut, was computed for each flatfish species within a trawl. The mean percent composition, based on numerical abundance, was determined also by averaging the percent composition of each individual fish gut for a given species within a trawl. When more than one trawl was examined from a sampling date, the frequency of occurrence and percent composition from the separate trawls were averaged to give an overall mean. Diversity (H') of prey consumed was computed using natural logarithms (Pielou 1969).

On two sampling dates, 29 May and 30 June 1979, English sole were captured at the study site and returned live to the laboratory along with sand collected from the same area using a 0.25 m^2 box core. Fish were placed in aquaria with the sediments, and their behavior was monitored over several days while they fed on naturally occurring prey in the sediments. Fresh seawater (12°C) was circulating continually through each aquarium. A photoperiod matching that experienced by the fish in the field was maintained using room lighting.

Quantitative meiobenthic samples were obtained from the study area at one site in 25 m of water (Fig. 1). Three replicate 0.25 m^2 box cores, positioned 30 m apart, were collected on each of six cruises between July 1978 and May 1979. Box cores were subsampled with at least three randomly placed clear plastic cores (1.9 cm internal diameter) which were in turn vertically partitioned into six depth increments (0-1 cm, 1-3 cm, 3-6 cm, 6-11 cm, 11-18 cm, and >18 cm). These plastic corers were also used to subsample Smith-McIntyre grabs collected on two cruises in July and September 1979 at the same site. Samples were preserved in 10% buffered Formalin and stained with rose bengal. The fauna was extracted from the sediments (well-sorted fine sand) by shaking and decanting followed by three rinses. A 38.5 μm sieve was used to retain the fauna. Harpacticoid copepods and nematodes were identified to species and enumerated.

RESULTS

The data for all four flatfish species are summarized in Table 1. A total of 422 guts from recently settled fish (17-88 mm SL) were examined, only 16 of which were empty (4%). The guts of an additional 40 late stage IV and early stage V *P. vetulus* larvae (sensu Shelbourne 1957) were also examined. These metamorphosing individuals, ranging in size from 16 to 18 mm SL, all had empty stomachs and intestinal tracts.

The 13 prey categories identified (Table 1, top) were placed into three broad groupings based on the size of individual food items and their typical location within the habitat. Small benthic prey were composed of palps from the surface deposit-feeding polychaete *Magelona sacculata*, juvenile bivalves (predominantly *Tellina modesta* and occasionally *Siliqua patula*), siphon tips cropped from tellinid clams, harpacticoid copepods (mainly *Halectinosoma* spp. and a few *Thompsonula hyaenae* and *Rhizothrix curvata*), free-living nematodes (*Theristus* sp. and *Mesacanthion* sp.), and tube feet from the sand dollar *Dendraster excentricus*. These food items were on the order of 0.5-1.5 mm long. Larger benthic prey were amphipods (predominantly *Ampelisca* spp. and *Eohaustoris* sp.), cumaceans, decapods (juvenile *Cancer magister*, pinnotherid crabs, and *Callianassa californiensis*), and polychaetes (*Nephtys* sp., *Glycinde armigera*, *Magelona sacculata*, *Thalenessa spinosa*, and *Spiophanes bombyx*). These prey were usually juveniles measuring 1.5-4 mm in their largest dimension. Species identifications were difficult for this latter group because of their immature status and tendency to fragment after being eaten. Examina-

TABLE 1.—Summary of data collected for English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, are the number of fish out of the total examined which had empty guts. The two values listed for each prey category are average

Species and date	No. tows examined	No. fish examined	Length range (mm)	Small benthic prey					
				Magelona palps	Juvenile bivalves	Tellinid siphons	Harpacticoid copepods	Nematodes	*Dendraster* tube feet
English sole									
12 May 1977	1	12 (1)	18-29	0.08 (0.64)	0.42 (0.91)	0.22 (0.73)	0.22 (0.82)	— (0.18)	
23 June 1977	1	16 (0)	19-48	0.01 (0.19)	— (0.19)	0.18 (0.56)	0.42 (0.69)	— (0.06)	
12 June 1978	1	3 (0)	22-24	0.04 (0.33)	0.88 (1.0)		0.04 (0.66)	0.02 (0.33)	
15 June 1978	1	5 (0)	20-25	0.59 (1.0)	0.17 (0.80)		0.14 (1.0)	0.05 (0.40)	
13 July 1978	2	14 (0)	19-46	0.46 (0.89)	0.24 (0.83)	0.08 (0.33)	0.18 (0.70)	— (0.06)	
25 July 1978	1	12 (0)	24-84	0.09 (0.75)	0.01 (0.08)		0.17 (0.42)	0.40 (0.67)	
5 Sept. 1978	1	3 (0)	45-58		1.0 (1.0)				
14 Nov. 1978	1	5 (0)	18-21	0.99 (1.0)					
23 Jan. 1979	4	24 (2)	17-34	0.72 (0.94)	0.05 (0.25)	— (0.06)	0.13 (0.52)		
22 Mar. 1979	2	20 (0)	19-35	0.02 (0.50)	0.80 (1.0)	0.02 (0.36)	0.14 (0.90)		
18 Apr. 1979	2	27 (1)	19-38	0.10 (0.50)	0.20 (0.73)	0.17 (0.61)	0.23 (0.67)	— (0.22)	
29 May 1979	4	37 (5)	18-42	0.07 (0.24)	0.20 (0.25)	0.24 (0.38)	0.20 (0.41)	0.05 (0.19)	
30 June 1979	2	23 (1)	18-61		0.01 (0.50)	— (0.09)	0.14 (0.75)		0.61 (0.75)
19 July 1979	3	10 (0)	27-62		0.20 (0.25)		0.30 (0.79)		
8 Aug. 1979	2	11 (0)	30-87		0.26 (0.19)	0.03 (0.06)	0.03 (0.19)		
24 Sept. 1979	2	13 (0)	46-82		0.02 (0.07)		0.10 (0.35)		
Total		235 (10)							
$\bar{x}$ 1979				0.11 (0.27)	0.22 (0.41)	0.06 (0.20)	0.16 (0.57)	0.01 (0.05)	0.08 (0.09)
Butter sole									
23 June 1977	1	6 (1)	18-23	0.01 (0.20)		0.25 (0.80)	0.47 (0.80)		
15 June 1978	1	16 (0)	19-30	0.62 (0.87)	0.13 (0.60)	0.01 (0.13)	0.01 (0.27)	0.05 (0.47)	
25 July 1978	1	16 (0)	22-31	0.44 (0.75)	0.06 (0.12)		0.24 (0.82)	0.13 (0.57)	
29 May 1979	3	14 (2)	17-35	0.04 (0.10)	0.15 (0.50)	0.25 (0.62)	0.17 (0.63)	0.11 (0.25)	
30 May 1979	1	4 (0)	49-60		0.03 (0.25)		0.03 (0.25)		
19 July 1979	3	7 (0)	21-88	— (0.08)	0.38 (0.58)		0.11 (0.33)		
8 Aug. 1979	4	9 (1)	24-34	0.02 (0.38)	0.43 (0.50)	— (0.13)	0.47 (0.58)		
Total		72 (4)							
$\bar{x}$ 1979				0.02 (0.12)	0.25 (0.46)	0.06 (0.19)	0.20 (0.45)	0.03 (0.06)	
Speckled sanddab									
23 June 1977	1	4 (0)	34-44			0.41 (0.75)	0.13 (0.25)		
25 July 1978	1	5 (0)	41-65						
22 Mar. 1979	1	10 (0)	29-39		0.08 (0.10)	0.01 (0.10)	0.10 (0.10)		
18 Apr. 1979	1	10 (0)	29-38						
29 May 1979	2	14 (0)	33-50	0.13 (0.13)					
30 June 1979	1	7 (0)	30-52						
19 July 1979	2	11 (1)	35-70						
24 Sept. 1979	3	15 (0)	38-70						
Total		76 (1)							
$\bar{x}$ 1979				0.02 (0.02)	0.01 (0.02)	— (0.02)	0.02 (0.02)		
Sand sole									
22 Jan. 1979	2	6 (0)	30-38						
18 Apr. 1979	1	3 (0)	29-55						
19 July 1979	2	6 (0)	29-50						
8 Aug. 1979	2	13 (0)	31-52						
24 Sept. 1979	2	11 (1)	30-48						
Total		39 (1)							
$\bar{x}$ 1979									

tion of the meiofaunal cores revealed that all the organisms classified as "benthic" occurred in the upper 1 cm of sediment. Prey items which were never found in benthic samples were defined as "pelagic" and consisted of mysids (mainly *Neomysis kadiakensis*), calanoid copepods (*Pseudocalanus* sp.), and veliger larvae. This distinction between benthic and pelagic organisms is somewhat arbitrary, since some of these species are mobile epibenthic forms which probably occur both in the sediments and the overlying water.

Adequacy of the sample sizes used in determining food habits of the flatfish species was assessed using several techniques. The guts of 16 *Parophrys vetulus* (19-48 mm SL) and 16 *I. isolepis* (19-33 mm SL) were examined from each of two tows. These two species were selected because they fed on a much broader spectrum of prey than *Citharichthys stigmaeus* or *Psettichthys melanostictus* and hence are subject to greater sampling error. The cumulative number of prey categories encountered, expressed as a function of sample size, is shown in Figure 2. For both English sole and butter sole, after seven or eight fish had been examined, no new food categories were found. After examining only four fish, 75% of all food items had been collected. This qualitative consistency among guts is also reflected in the high frequency of occurrence (Table 1) for most prey. Quantitatively, the composition of gut

Citharichthys stigmaeus; and sand sole, *Psettichthys melanostictus*. Numbers in parentheses under the heading "No. fish examined" numerical percent composition and average frequency of occurrence (in parentheses). "—" indicates prey item <0.01.

Species and date	No. tows examined	No. fish examined	Length range (mm)	Large benthic prey				Pelagic prey		
				Amphipods	Cumacea	Decapods	Polychaetes	Mysids	Calanoid copepod	Veliger larvae
English sole										
12 May 1977	1	12 (1)	18-29	0.03 (0.27)		— (0.09)		0.01 (0.18)		
23 June 1977	1	16 (0)	19-48	0.15 (0.63)		0.24 (0.44)				
12 June 1978	1	3 (0)	22-24	0.01 (0.33)			0.01 (0.33)			
15 June 1978	1	5 (0)	20-25	0.02 (0.40)			0.04 (0.60)			
13 July 1978	2	14 (0)	19-46	0.02 (0.40)	0.01 (0.36)	0.02 (0.42)				
25 July 1978	1	12 (0)	24-84	0.18 (0.25)	0.04 (0.25)		0.03 (0.10)	0.04 (0.08)		
5 Sept. 1978	1	3 (0)	45-58							
14 Nov. 1978	1	5 (0)	18-21				0.01 (0.20)			
23 Jan. 1979	4	24 (2)	17-34	0.08 (0.52)	0.02 (0.14)			— (0.06)		
22 Mar. 1979	2	20 (0)	19-35	0.03 (0.60)	— (0.30)			— (0.10)		
18 Apr. 1979	2	27 (1)	19-38	0.25 (0.62)	0.04 (0.35)	— (0.03)		— (0.09)		
29 May 1979	4	37 (5)	18-42	0.03 (0.19)	0.03 (0.05)	0.17 (0.17)	0.02 (0.16)	— (0.13)		
30 June 1979	2	23 (1)	18-61	0.18 (0.54)	0.05 (0.25)	— (0.09)	— (0.09)			
19 July 1979	3	10 (0)	27-62	0.33 (0.70)	0.15 (0.50)	0.01 (0.08)				
8 Aug. 1979	2	11 (0)	30-87	0.45 (0.86)	0.21 (0.81)	0.01 (0.13)	— (0.33)	0.01 (0.06)		
24 Sept. 1979	2	13 (0)	46-82	0.29 (0.90)	0.41 (0.84)		0.18 (0.57)	— (0.09)		
Total		235 (10)								
$\bar{x}$ 1979				0.21 (0.62)	0.11 (0.41)	0.02 (0.06)	0.03 (0.14)	— (0.07)		
Butter sole										
23 June 1977	1	6 (1)	18-23	0.07 (0.80)				0.20 (0.20)		
15 June 1978	1	16 (0)	19-30	0.02 (0.33)	0.01 (0.20)		0.16 (0.87)			
25 July 1978	1	16 (0)	22-31	0.03 (0.25)	0.05 (0.38)		0.05 (0.38)	— (0.06)		
29 May 1979	3	14 (2)	17-35	0.04 (0.21)	0.03 (0.16)		0.03 (0.16)	0.05 (0.33)		
30 May 1979	1	4 (0)	49-60	0.32 (1.0)	0.26 (1.0)	0.29 (1.0)	0.07 (0.25)			
19 July 1979	3	7 (0)	21-88	0.21 (0.58)	0.04 (0.17)	0.18 (0.33)		0.08 (0.08)		
8 Aug. 1979	4	9 (1)	24-34	0.07 (0.54)	0.01 (0.63)			— (0.13)		
Total		72 (4)								
$\bar{x}$ 1979				0.16 (0.58)	0.09 (0.49)	0.12 (0.33)	0.03 (0.10)	0.03 (0.14)		
Speckled sanddab										
23 June 1977	1	4 (0)	34-44	0.20 (0.50)	0.13 (0.25)	0.11 (0.25)		0.03 (0.25)		
25 July 1978	1	5 (0)	41-65					1.0 (1.0)		
22 Mar. 1979	1	10 (0)	29-39	0.08 (0.30)	0.01 (0.10)			0.72 (0.80)		
18 Apr. 1979	1	10 (0)	29-38	0.20 (0.20)	0.52 (0.60)	0.03 (0.10)		0.25 (0.30)		
29 May 1979	2	14 (0)	33-50	0.25 (0.43)		0.30 (0.53)		0.32 (0.53)		
30 June 1979	1	7 (0)	30-52	0.03 (0.57)	— (0.05)	0.01 (0.29)		0.96 (1.0)		
19 July 1979	2	11 (1)	35-70	0.04 (0.20)				0.96 (1.0)		
24 Sept. 1979	3	15 (0)	38-70	0.14 (0.52)	0.08 (0.25)	0.20 (0.52)		0.59 (0.86)		
Total		76 (1)								
$\bar{x}$ 1979				0.12 (0.37)	0.10 (0.17)	0.09 (0.24)		0.63 (0.75)		
Sand sole										
22 Jan. 1979	2	6 (0)	30-38					1.0 (1.0)		
18 Apr. 1979	1	3 (0)	29-55					1.0 (1.0)		
19 July 1979	2	6 (0)	29-50					1.0 (1.0)		
8 Aug. 1979	2	13 (0)	31-52			0.03 (0.17)		— (0.13)	0.69 (0.80)	0.28 (0.40)
24 Sept. 1979	2	11 (1)	30-48					1.0 (1.0)		
Total		39 (1)								
$\bar{x}$ 1979						0.01 (0.03)		0.80 (0.83)	0.14 (0.13)	0.06 (0.08)

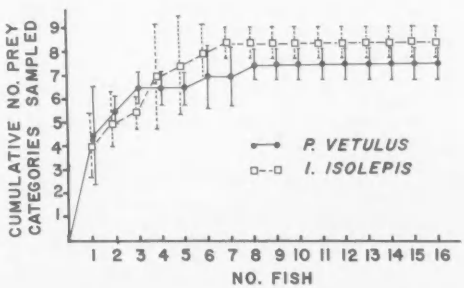

FIGURE 2.—Cumulative number of prey categories sampled as a function of sample size for *Parophrys vetulus* and *Isopsetta isolepis*. Each data point represents the mean of two separate trawl collections. Vertical bars are ±1 standard deviation.

contents varied little among individuals of a species within a trawl. For each species studied, food items from fish caught in the same trawl tended to have the same rank order of numerical abundance. This consistency of results was statistically significant; the null hypothesis of independence among prey rankings was rejected (Friedman's nonparametric randomized block ANOVA, $P<0.005$; Gibbons 1971). On several sampling dates the number of fishes available for study was small, e.g., *Parophrys vetulus* on 5 September 1978 (three fish), *I. isolepis* on 30 May 1979 (four fish). The small within-sample variability of these species, however, indicates that such small sample sizes will not unduly bias de-

termination of the major food items consumed.

As is apparent from Table 1, *P. vetulus* feeds on a wide variety of benthic animals. Juvenile bivalves, harpacticoid copepods, *Magelona* palps, and amphipods are particularly abundant in English sole guts. On most sampling dates, the frequency of occurrence of these four prey in the diet of English sole was high, although typically only one or two items dominated the diet numerically. Occasionally a food item which was usually rare became a major component in the guts of English sole, such as free-living nematodes on 25 July 1978 or echinoid tube feet on 30 June 1979. The diet of *I. isolepis* was very similar to that of *P. vetulus*, with the exception that butter sole fed to a greater extent on mysids and decapods. *Citharichthys stigmaeus* fed equally on large epibenthic crustaceans (amphipods, decapods, cumaceans) and pelagic prey. Polychaetes were totally lacking in the diet. *Psettichthys melanostictus* consumed mysids almost exclusively; only on 8 August 1979 were other pelagic prey found in the guts of this species. Average H' diversity of food consumed per sampling date in 1979 was 1.38 for English sole, 1.47 for butter sole, 0.81 for speckled sanddabs, and 0.14 for sand sole. The similarity in diets of these four species was compared by computing the percent similarity index (PSI; Whittaker 1960) based on the average 1979 proportions of prey consumed by each species (Table 2). Two of these paired comparisons, *Parophrys vetulus-I. isolepis* and *C. stigmaeus-Psettichthys melanostictus*, indicate similarities exceeding 50%. In the case of the speckled sanddab and the sand sole, this dietary overlap is based on their common utilization of one food category, mysids. English and butter soles share a wide variety of prey which were consumed in very similar proportions, e.g., 29 May 1979.

Observations of 20-25 mm *Parophrys vetulus* feeding in laboratory aquaria revealed two basic types of foraging behavior. In the first, fish remained motionless on the bottom and then periodically lunged forward 1-2 cm, striking at objects located on the surface of the sediment. In the second, fish slowly raised their heads above the bottom then rapidly thrust forward, causing the upper few millimeters of sediment to billow into suspension. *Parophrys vetulus* would then strike in rapid succession at small objects presumably temporarily displaced from the bottom. Neither type of behavior predominated; both were detected in all of the individuals observed. After monitoring these responses for several hours, fish were sacrificed and the guts examined. Harpacticoid copepods dominated the diet of these fish.

Shifts in prey preference as a function of fish size (age) were observed in English sole. The average diets of all *P. vetulus* less than and greater than 35 mm SL were computed using the 1979 data and then compared (Table 3). The dramatic difference in prey of these two size classes is apparent. Smaller fish (17-35 mm SL) consumed small prey almost exclusively, while larger fish (35-82 mm SL) only occasionally ingested these small items, choosing instead amphipods and cumaceans. *Isopsetta isolepis* showed a similar shift in the preferred size of prey as standard length increased from 30 to 40 mm. Fourteen butter sole (17-35 mm SL) caught on 29 May 1979 fed predominantly on small food items, while the gut contents of four larger fish (49-60 mm SL) caught 1 d later were composed of amphipods, cumaceans, and decapods (Table 1). A similar distinction was found in fish collected on 19 July 1979. Neither *C. stigmaeus* nor *Psettichthys melanostictus* altered the taxonomic composition of their diet within the size ranges of fish we examined, although, as with English and butter soles, larger fish ate larger prey.

The guts of all four species were generally <25% full in the morning before 0900 h. Stomach fullness gradually increased during the late morning and afternoon. The correlation between

TABLE 2.—Percent similarity of prey consumed by English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*, based on the average 1979 diets shown in Table 1.

Species	*I. isolepis*	*C. stigmaeus*	*P. melanostictus*
P. vetulus	0.77	0.29	0.01
I. isolepis	—	0.39	0.05
C. stigmaeus	—	—	0.64

TABLE 3.—Mean numerical proportions of dominant prey items in the guts of *Parophrys vetulus* less than and greater than 35 mm SL.

	SL <35 mm	SL >35 mm
Small benthic prey		
Magelona palps	0.28	0.03
Juvenile bivalves	0.29	0.01
Tellinid siphons	0.13	0.01
Harpacticoid copepods	0.16	0.08
Total	0.86	0.13
Large benthic prey		
Amphipods	0.08	0.46
Cumaceans	0.03	0.30
Decapods	0.01	0.04
Polychaetes	0.0	0.06
Total	0.12	0.86

the time of capture (ranging between 0830 and 1800 h) and average gut fullness for English sole was significant; $r = 0.49$, $P = 0.05$. On 22 March 1979 two otter trawl hauls were made, one at 1000 and another at 1800 h. Guts of 10 English sole ranging in size between 19 and 35 mm SL were examined from both trawls. The diets of both groups of fish were the same, but the fish collected at 1800 h had an order of magnitude more food items in their guts than the earlier collection: 90% full, 198±56 SD items, vs. 10% full, 18±17 SD items. *Isopsetta isolepis*, *C. stigmaeus*, and *P. melanostictus* showed similar daily trends.

Sufficient numbers of English sole of the same size were collected on 23 January and 29 May 1979 to compare the similarity of diets within and between replicate trawls. The PSI was used to quantify the proportion of food items found in common for each possible pair of fish collected on a sampling date. Mean similarity values were then obtained by averaging the PSI values for the fish within the same trawl and for fish collected in different trawls. Comparing replicate samples obtained at the same depth (Table 4), the average PSI for fish guts within the same trawl in both January and May, as well as the mean PSI between fish in different trawls in January, were approximately the same, 50%. The similarity between two trawls at the same depth in May, though, is very low (3%). Table 4 (bottom) also shows a comparison of within-trawl and between-trawl similarity, where trawls were collected at different depths (20 m and 30 m). Again the within-trawl affinities are high in both January and May, as is the between-tow similarity in January. The average PSI in May for fish from different depths is low. The increased between-trawl variability in food habits noted on 29 May was a general feature observed in all late spring and early summer replicate collections of *Parophrys vetulus*. For example, on 13 July 1978, trawls were made at 15 m and 20 m. *Magelona* palps numerically comprised 72% of the English sole diet at 15 m but only 19% at 20 m, while juvenile bivalves and harpacticoid copepods combined to form 19% of the prey consumed at 15 m and 63% at 20 m.

TABLE 4.—Average percent similarity of index of *Parophrys vetulus* diets within and between replicate trawls on 23 January and 29 May 1979.

	Replicates at same depth		Replicates at different depths	
	Within trawl	Between trawl	Within trawl	Between trawl
23 January 1979				
20 m	53%	53%		
20 m and 30 m			71%	66%
29 May 1979				
10 m	50%	3%		
20 m and 30 m			65%	12%

The diet of recently settled English sole changed continually among sampling months. Comparing similar-sized fish (17-35 mm SL) caught in 1979 (Fig. 3) reveals that dominant food items on a numerical basis varied from *Magelona* palps (November 1978, January 1979), juvenile bivalves (March 1979), bivalve siphons (April and May 1979), to juvenile bivalves and harpacticoid copepods (July 1979). Examination of samples collected in 1977 and 1978 showed that the sequence of changes noted in 1979 does not repeat each year. *Magelona* palps, which in 1979 were never a dominant item in the diet of *P. vetulus* after January, were numerically the most abundant food on two sampling dates in the summer of 1978. Other between-year differences exist, e.g., 5 September 1978 and 24 September 1979, but it is impossible to determine whether these differences are real or a result of spatial variability in diet combined with insufficient sampling.

The apparent increased equitability of prey items shown in Figure 3 for April and May relative to January and March does not indicate that spring and summer diets of individual fish are more diverse than in winter. Instead, the difference is an artifact of the spatial variability previously noted, being generated by averaging the data for all fish caught in different tows. The average dietary diversity (H') of an individual fish on 23 January 1979 (0.43±0.35 SD, $n = 24$) was not significantly different from that on 29 May 1979 (0.37±0.41 SD, $n = 32$).

The only seasonal data currently available on the abundance of benthic organisms at Moolach Beach are for nematodes and harpacticoid copepods. Nematodes are very abundant ($\bar{x} = 1{,}050 \cdot 10\ \text{cm}^{-2}$), but quantitatively, with the exception of one sampling date, are not significant in the diet of the fish species we studied. Harpacticoids are important in the diets of English and butter soles, yet are not abundant at the study site. Their average density for the eight sampling dates between July 1978 and September 1979 was 12.2±4.0 SE $\cdot$ 10 cm^{-2}. Only the larger species found in the 0-1 cm depth increment were present in fish guts. *Halectinosoma* spp. comprised more than 80% of all harpacticoid prey.

Seasonally, *Halectinosoma* ranged in abundance from a mean of 6.8 · 10 cm^{-2} between May and September ($n = 5$) to zero from October to March ($n = 3$). Their period of maximum density coincides with their maximum occurrence in the diet of 17-35 mm SL English sole (Fig. 3).

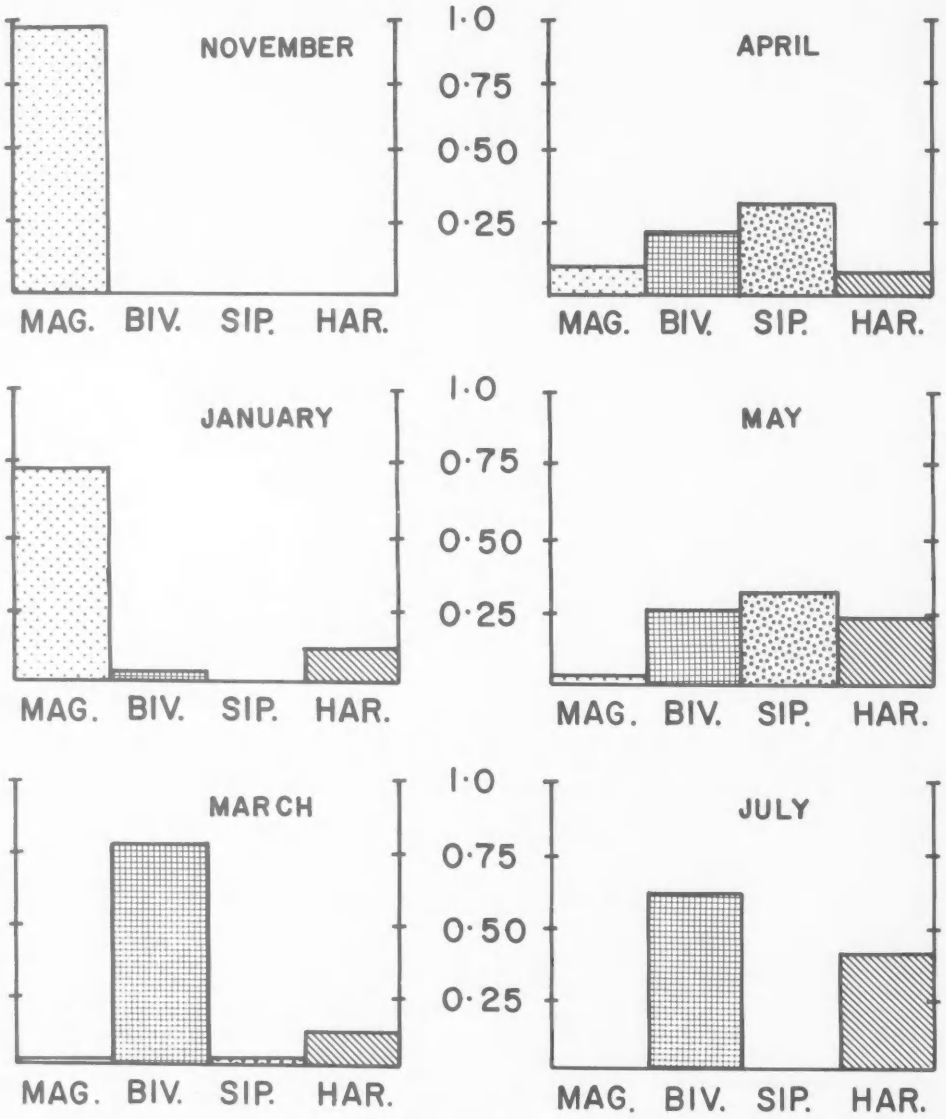

FIGURE 3.—Seasonal change in food habits of *Parophrys vetulus* <35 mm SL between November 1978 and July 1979. Vertical bars indicate average proportion of *Magelona* palps (Mag.), juvenile bivalves (Biv.), clam siphons (Sip.), and harpacticoid copepods (Har.) in the diet.

DISCUSSION

The diet of recently settled English sole is a function of size, location of capture, and season (Tables 1, 3, 4). Both the within-year and between-year differences in diet noted for *P. vetulus* are similar to changes documented for other pleuronectid species (Macer 1967; Edwards and Steele 1968) and are probably related to temporal changes in density of prey organisms. Steele et al. (1970) concluded that variations in predation on *Tellina* siphons and polychaetes by young plaice, *Pleuronectes platessa*, were a result of changes in both the absolute and relative abundances of these prey over time. The observed relationship between seasonal changes in harpacticoid copepod abundance and the utilization of these prey as food by English sole is the only direct evidence we have to support this contention. However, the juvenile bivalves (*Tellina* and *Siliqua*) consumed by *Parophrys vetulus* were all young of the year which are known to have temporally variable recruitment (Jones[5]), suggesting that seasonal availability of this food item is also not constant. Moreover, Oliver et al. (1980) seasonally sampled the nearshore macrobenthos in a region of Monterey Bay, Calif., which was very similar to Moolach Beach in terms of physical environment and fauna present. Their results indicate that the abundance of amphipods and such polychaetes as *Magelona sacculata* vary both within and between years. English sole at Moolach Beach probably alter their diet over time in accordance with similar temporal changes in the density of these larger prey species, but additional benthic data obtained concurrently with fish collections are necessary to substantiate this conclusion.

The marked differences between summer and winter spatial variability in English sole diets (Table 4) are thought to be related to changes in both the abundance and spatial distribution of prey. During the winter, intense storm activity along the Oregon coast produces large waves which continually disturb and mix the sediments of the inner continental shelf (Komar et al. 1972). The meiobenthos has been shown to become randomly distributed during these periods within small areas (1 m^2) and only slightly aggregated on larger scales (Hogue 1982). Small benthic prey fed upon by 0-age English sole would most likely be affected by this vigorous physical mixing in much the same way as the meiofauna. As a result, English sole feeding at either the same depth or different depths may consume similar prey in the winter (Table 4, January) because prey organisms are more evenly distributed within the study area compared to other times of the year. Such a distribution, when coupled with the numerical dominance of one food item, would increase the similarity of food items available for consumption throughout the region. During the late spring and summer the physical disruption of sediment is minimized and the spatial distribution of the meiofauna becomes increasingly aggregated (Hogue 1982). Distinct differences in the species composition and abundance of nematodes and harpacticoids have been found at locations only 250 m apart. During this period there is little similarity in diets of English sole from replicate trawls (Table 4, May). In the spring and summer, *P. vetulus* may be opportunistically exploiting different prey which are densely aggregated in different sectors of the Moolach Beach site.

Seasonal changes in the spatial distribution of prey items may also alter the rate at which prey are consumed. Experiments with fish feeding in aquaria (Ivlev 1961) have shown that an increase in the degree of aggregation of food sources has the same effect on the rate of food consumption as an increase in the concentration of food. Results of Tinbergen et al. (1967) suggest similar relationships between the spatial distribution of prey and predation. Fish commencing their benthic feeding in the late spring and summer at Moolach Beach may benefit energetically from the increased aggregation of benthic organisms during this period relative to that found during the winter.

The consumption of parts of macrobenthic organisms, e.g., *Magelona* palps and tellinid clam siphons, rather than whole individuals by English sole <35 mm in length is probably related to the maximum size of food items capable of being captured and ingested by these fish. We measured the mouth size of 30 mm *P. vetulus* and found that prey greater than about 2 mm in their largest dimension are too large to be consumed by such small fish. Siphons and palps are apparently the only portion of larger prey which are available for ingestion by fish <35 mm SL. As fish grow larger than 35 mm, small food items are neglected in favor of polychaetes, amphipods, and cumaceans which yield far more en-

[5]H. R. Jones, School of Oceanography, Oregon State Univ., Corvallis, OR 97331, pers. commun.

ergy per individual item. Two fortuitous consequences of this size-dependent predation may be important. First, the dietary overlap between small juveniles and larger fish is minimized, thus conserving food stocks for recently settled individuals. Second, both siphons and palps are capable of being regenerated. By consuming only parts of benthic organisms, food sources are not destroyed and may be cropped again in later months by other individuals following regeneration. This may be particularly important in the case of English sole because juveniles are continuously recruited to the bottom over a 9-mo period (Krygier and Pearcy footnote 2).

The four pleuronectiform fishes we studied form a trophic continuum, ranging from generalists feeding upon numerous benthic prey (*P. vetulus*) to specialists relying on a few pelagic food items (*Psettichthys melanostictus*). *Isopsetta isolepis* and *C. stigmaeus* are intermediate in their position on the continuum. Few published results exist with which to compare ours. Cailliet et al. (1979) investigated the food habits of *Parophrys vetulus*, *C. stigmaeus*, and *Psettichthys melanostictus* at an ocean station in Monterey Bay. The fish they examined were all larger than the ones for which we have data, but the same basic trends emerge. They found that English sole was a generalist, eating a wide variety of benthic food items; sand sole relied almost totally on mobile crustaceans for food; and speckled sanddab fed on pelagic and epibenthic crustacea and occasional infaunal worms and molluscs. Wakefield (footnote 3) has studied the adult food habits of these three species as well as those of *I. isolepis* collected at the Moolach Beach site. Although the specific food items ingested differ for recently settled juveniles and adults at this site, the basic modes of feeding, e.g., infaunal generalist or pelagic specialist, remained unchanged at Moolach Beach as the youngest juveniles mature to adults.

The greatest similarity among diets is between those of *Parophrys vetulus* and *I. isolepis*. Both of these benthophagous species have similar mouths with small, asymmetrical jaws and small incisor teeth. Both complete metamorphosis and commence benthic feeding at the same size (18-20 mm SL). Qualitatively there is no difference in their diet, although quantitatively butter sole occasionally feed more heavily on mysids. Comparing fish of the same size (17-35 mm SL) on 29 May 1979, *P. vetulus* and *I. isolepis* fed on the same prey items in the same proportions. If food should be limiting for these two species, then in the absence of subsequent shifts in food preference the potential exists for competitive interaction. While observing the feeding behavior of *P. vetulus* in the laboratory, several butter sole were placed in the aquaria along with the English sole. *Isopsetta isolepis* were observed to bite the fins of *P. vetulus* and pursue them around the tank. These were casual observations which were only replicated over a 2-d period. Should this aggressive behavior be substantiated by further work, then interference competition between *P. vetulus* and *I. isolepis* in the Moolach Beach area seems likely. On the whole, however, English and butter soles do not settle at the same time or place. *Parophrys vetulus* has a protracted benthic recruitment period, settling to the bottom between November and July in estuarine and coastal waters <30 m deep (Krygier and Pearcy footnote 2). *Isopsetta isolepis*, on the other hand, has a restricted settling period (May-August) yet occurs over a broader depth range (9-60 m) (Krygier and Pearcy footnote 2). If interspecific interactions were occuring between English and butter soles, it is likely that they would be limited to regions of overlap like Moolach Beach in the summer months.

ACKNOWLEDGMENTS

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PRESSURE SENSITIVITY OF ATLANTIC HERRING, *CLUPEA HARENGUS* L., LARVAE[1]

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ABSTRACT

Larval Atlantic herring, *Clupea harengus harengus* L., are known to change their vertical distribution by day and night, but it is not clear if they can sense their depth by perception of hydrostatic pressure. Two experiments were designed to test whether herring larvae would respond to imposed pressure changes by making appropriate compensatory vertical movements and whether such ability could be related to the development of the bulla system (stage I, bulla absent; stage II, bulla liquid-filled; stage III, bulla gas-filled). In the first experiment, pairs of larvae were exposed to a fixed sequence of pressure changes (ΔP) from ±13 cm H_2O to ±66 cm H_2O. Members of simultaneously tested pairs tended to be influenced by one another when responding to pressure change. The response of stage-I larvae tended to first increase and then decrease over a 20-min test period for a given ΔP. Stage-II and stage-III larvae showed better performances in compensating for imposed pressure changes than did stage I. Larvae exposed to a sudden pressure increase of 5 atm (atmospheres) (5,000 cm H_2O) before the experiment did not perform as well as those not so exposed, but the differences were not statistically significant. A second experiment tested the response of individual larvae to randomized sequences of pressure changes. Stage-III larvae moved most frequently to compensate for the pressure changes, but stage-I and stage-II larvae also responded to changes in pressure. Both experiments show that herring larvae of all three stages compensate for applied pressure changes by moving up when pressure is increased and down when it is decreased, but that they rarely move sufficiently far in the vertical plane to fully compensate.

Larval fish are known to change their vertical distribution diurnally. Although this behavior is probably controlled by changes in light intensity, it is not clear whether hydrostatic pressure perception is important in limiting or controlling the depths reached at different stages of the vertical migration cycle. A few workers (e.g., Qasim et al. 1963) have shown that fish larvae can respond to pressure changes; in particular, Bishai (1961) and Blaxter and Denton (1976) have shown that Atlantic herring, *Clupea harengus harengus* L., larvae are pressure sensitive.

The most likely site for a pressure receptor is a gas-filled structure, such as a swim bladder, which, if compliant, undergoes large changes in volume during vertical movements (10 m change of depth being equivalent to 1 atmospheric pressure). However, clupeoids, together with some other groups such as mormyrids, have gas-filled bulla. In herring the bulla appears to be sensitive to pressure changes (Allen et al. 1976; Denton and Blaxter 1976). In herring the prootic bulla has two parts: one filled with gas, the other with perilymph. The two parts are separated by an elastic membrane. This membrane responds to pressure changes, driving the perilymph in or out of a fenestra, which is situated close to the utriculus of the inner ear. The gas-filled part of the bulla is also connected to the swim bladder by a very narrow gas duct. This connection allows the prootic membrane to adapt to slow changes of pressure. If the pressure increases, the membrane bows in and being elastic tends to return to its resting position. The swim bladder wall is compliant and the pressure differential created along the gas duct causes gas to flow into the bulla from the swim bladder. If the pressure decreases, the membrane bows outward (into the perilymph space) and gas flows from the bulla back to the swim bladder.

In the fully functional system described above the bulla may respond to hydrostatic pressure changes, but because the system adapts in 15-30 s, there will be no perception of absolute pressure. In the very early larval stages of herring (from hatching to 18 mm TL) no bulla is present; the bulla appears at about 18 mm and usually is filled with gas by 26 mm. The swim bladder is not fully formed until 35 mm or more (Blaxter

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and Denton 1976). One would predict that herring larvae up to 18 mm would have little or no pressure sensitivity. As the bulla becomes filled with gas but before the swim bladder develops, we would expect very high sensitivity to absolute pressure (no adaptation being possible) and herring larvae from 26 to 35 mm would be in this category. Larger larvae would retain sensitivity to pressure change, but the development of the adaptation mechanism would prevent its being an absolute sense. One also would predict that herring larvae with gas-filled bullas but no swim bladders would be especially vulnerable to large pressure changes that could cause the membrane to burst. Hoss and Blaxter (1979) have shown that herring larvae do appear to be especially vulnerable to large, rapid pressure changes at about this stage of the life history. Blaxter and Hoss (1979) followed the development of the adaptation mechanism, measured its time constant, and have shown that adaptation usually does not develop until a length of >30 mm.

This paper describes a detailed analysis of pressure sensitivity in herring larvae, using the hypothesis that a larva will swim up to compensate for increasing pressure and down to compensate for decreasing pressure and that this is due in part to the development of the bulla system. In the two experiments to be described, particular attention was paid to measuring changes in sensitivity during the development of the bulla-swim bladder system. In addition, the effect of a large, rapid pressure change on subsequent pressure sensitivity also was investigated in one experiment.

MATERIALS AND GENERAL METHODS

Herring were reared from fertilized eggs, using the techniques of Blaxter (1968). The temperature during development increased from about 7°C near hatching to 12°C, 4 or 5 mo later. The pressure sensitivity experiments were conducted in a constant temperature room at 9°-10°C, using the apparatus of Blaxter and Denton (1976). This apparatus consisted of a Plexiglas[4] cylinder 80 cm high and 7 cm in diameter, the transparent wall being marked on the outside to give 16 equal sections numbered 1-16. The surface was designated 0, the bottom as 17. This allowed an observer to record the position of a larva in the cylinder at any given instant with a number from 0 to 17. The pressure in the cylinder could be changed by a preset amount by opening a two-way tap at the top, which exposed the water surface to atmospheric pressure or to positive or negative pressures in a gas reservoir.

Each larval herring was anesthetized after it was tested and the developmental stage of its bulla (stage I, no bulla; stage II, bulla liquid-filled; stage III, bulla gas-filled) was ascertained. A complication arose that the bulla does not become instantaneously filled with gas and may contain only a few or many bubbles. Pressure sensitivity is more likely to be high if the bulla is full of gas. At least 10 larvae of each developmental stage were used.

EXPERIMENT I

Design

Pairs of larvae of approximately equal length and stage of development were tested simultaneously. After a 2-3 min acclimation period at atmospheric pressure, 10 observations on the position of each fish were made at 15-s intervals. The pressure was then changed and the observations were repeated at the new pressure.

The pressure sequence selected was based upon prior research (Blaxter and Denton 1976) and involved changing the pressure from atmospheric to each of the following pressures four times: ±13, ±39, and ±66 cm H_2O (1 cm H_2O = 0.001 atm), for a total of 480 observations and 47 changes of pressure (Fig. 1). This fixed sequence of increasing pressure differentials was chosen to avoid the potential danger of larvae becoming overstimulated initially at the higher pressures. Earlier evidence (Blaxter and Denton 1976) indicated that larvae moved upwards to compensate for increased pressure and downwards to compensate for decreased pressure, and the extent of vertical movement was correlated with the extent of pressure change (ΔP) applied. Large pressure changes early in the sequence might not only block responses to smaller subsequent pressures but might also cause earlier fatigue. Therefore, pressure changes were not randomized and an experiment commenced regardless of larval distribution in the water column. Approximately half the larvae used in Experiment I were preexposed for 1 min to an abrupt pressure increase

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

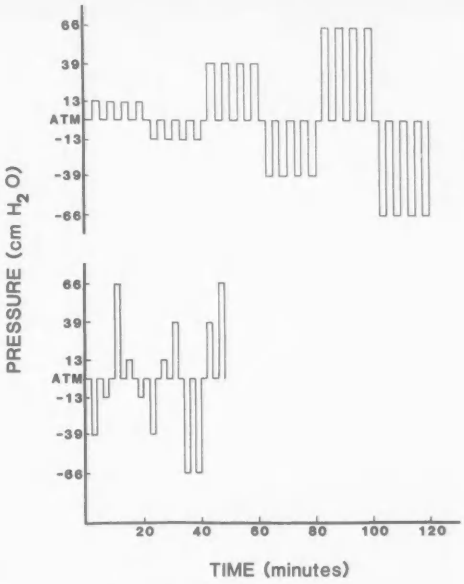

FIGURE 1.—The upper figure depicts the fixed pattern of pressure changes to which pairs of larval herring were exposed in Experiment I. The lower figure shows an example of one of the randomized sequences of pressure changes to which a larval herring was exposed in Experiment II. An independently randomized sequence was drawn for each larval herring tested.

of 5 atm (5,000 cm H_2O) before the onset of the regular pressure series to determine if this abrupt ΔP would impair subsequent pressure sensitivity differently in the different developmental stages. These are referred to as treated larvae, whereas those not preexposed are referred to as control larvae.

Results

Although pairs of larvae selected for simultaneous testing were judged visually to be of equal length, the developmental status of their bulla systems was evaluated only after they were subjected to the pressure tests and was sometimes found to differ (Table 1).

A total of 480 locations within the cylinder were recorded for each herring tested. We averaged 10 locations of a larva during a 2.5-min test at a given pressure to obtain a more concise summary of the response pattern. We then assigned a score to the larva for each 2.5-min series: +, if its average position indicated it had moved in the vertical direction to compensate for the change in pressure; −, if it moved in the opposite direction; and nr, if it showed no net change in its vertical position. We have used these assigned scores in the analyses to follow. Larvae not responding were treated as if they had moved in the noncompensatory direction, so the analyses are conservative. The scoring technique allows one to evaluate the frequency with which a fish, contending with a dynamic pressure regime, moved correctly, i.e., moved in the appropriate vertical direction to compensate for the imposed pressure change.

A separate analysis of variance of the number of compensatory responses was calculated for each treatment group, using only the data for members of homogeneous pairs to determine whether the paired larvae tend to respond together. The intraclass correlation coefficients ranged from 0.91 to 0.92 for the two stage-I groups to 0.20 and 0.32 for the two stage-III groups, respectively (Table 1). Thus for the least, well-developed fish (stage I) the variation among members of a pair was only one-ninth as great as the variation between average values for pairs of fish, i.e., the two members of a pair tended to respond together as a unit. The stage-II control group was an exception to this general pattern. For that group the variation among members of a pair was greater than the variation among pairs, suggesting that the members of a pair tended to move away from one another as pressure within the cylinder was changed.

The lack of independence in the responses of fish tested simultaneously invalidates use of the data for mixed pairs (i.e., pairs of fish of different developmental stages) and requires that we consider pairs of larvae as the experimental unit in testing hypotheses about the average performances. An analysis of variance of data for homo-

TABLE 1.—Numbers of herring larvae, numbers of pairs of larvae of the same developmental stage, and intraclass correlation coefficients for fish tested in Experiment I.

	Control	Preexposed to 5 atm (treated)
Stage I		
Number of individuals	9	8
Number of homogeneous pairs	4	4
Intraclass correlation coefficient	0.92	0.91
Stage II		
Number of individuals	15	11
Number of homogeneous pairs	4	4
Intraclass correlation coefficient	−0.42	0.41
Stage III		
Number of individuals	10	11
Number of homogeneous pairs	2	4
Intraclass correlation coefficient	0.20	0.32

geneous pairs disclosed that stage-I fish moved vertically to compensate for the imposed pressure changes less often than those possessing a more developed bulla system (Table 2). No advantage for fish possessing gas-filled bullas rather than liquid-filled bullas was detected. Although there was a consistent tendency for herring previously exposed to 5 atm to move vertically to compensate less frequently than those not so exposed, this tendency was not statistically significant. The overall intraclass correlation coefficient was 0.67, implying that the average variation among pairs within a treatment group was twice that between members of a pair.

The hypothesis testing reported above ignores the fact that a larval herring could respond in three ways to the 47 changes in pressure; it could move vertically to compensate, it could move vertically in the opposite direction, or it could simply maintain its current position within the cylinder. A plot of the data for pairs of larvae shows that nonresponse to changing pressure was more frequent for stage-I larvae than for the more developed fish (Fig. 2). Two pairs of larvae in particular, one for the stage-I control group and one from the stage-I treated group, are clearly outliers, showing no response during 49% and 86% of the trials, respectively. If these two pairs are dropped from the analysis, then the differences reported above are no longer significant and the means are 27.7 and 25.2, respectively (instead of 23.8 and 19.8) and are close to those for the corresponding stage-II groups (Table 2).

A plot of moving averages of the percentage of compensatory responses against the sequential series of pressure changes reveals that the stage-I herring exhibited a rather consistent pattern of

TABLE 2.—Analysis of variance of number of compensatory moves of fish during pressure sensitivity tests, and table of means: I = bulla absent, II = bulla liquid filled, III = bulla gas filled.

Source	df	Mean square	F
Preexposure	1	45.47	0.49
Developmental stage	2	314.26	3.40
II versus III	1	88.05	0.95
I versus II and III	1	540.47	5.85*
Interaction	2	28.48	0.31
Experimental error	16	92.44	5.08**
Sampling error	22	18.20	

Intraclass correlation coefficient = 0.67

Average number of compensatory moves per fish:

	Control	Preexposed to 5 atm
Stage I	23.8 (51%)	19.8 (42%)
Stage II	28.9 (61%)	26.1 (56%)
Stage III	32.2 (68%)	30.5 (65%)

*$P<0.05$; **$P<0.001$.

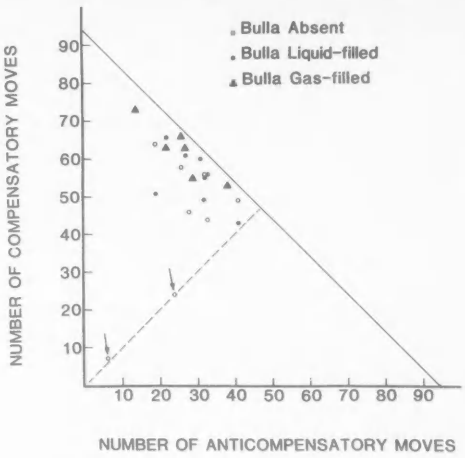

FIGURE 2.—Total numbers of compensatory vertical movements of a pair of herring plotted against the corresponding number of anticompensatory movements for that pair. The dashed line indicates the evenly divided response expected under the null hypothesis. Nonresponse is indicated by the vertical (or horizontal) distance from the hypotenuse. Control and preexposed pairs are not plotted separately. Arrows indicate two outliers.

response over the 20 min test period for a given ΔP, especially for the larger ΔP's (Fig. 3). Performance improved at the onset of a new increment or decrement of pressure and then fell off as the test continued, only to improve when the next increment or decrement was used. The other two developmental stages showed a relatively high initial frequency of compensation that rapidly decreased, then subsequently increased until the test of the final pressure change.

Discussion

The results in Figures 2 and 3 clearly show that some larvae are responsive to pressure. However, the relatively small sample size, the correlation in the behavior between members of a pair simultaneously tested, and the relatively high variation in response among experimental units within a given treatment group reduced our ability to distinguish differences in the response to changes in pressure of herring of different developmental stages. Additional problems in interpreting the first experiment arose from the evidence that tests of a given pressure

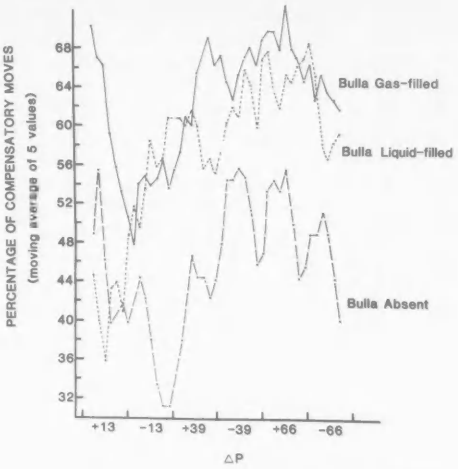

FIGURE 3.—Moving averages of the percentage of correct vertical movements for the three developmental stages of herring in the first experiment. Data for control and preexposed herring are not plotted separately.

change were too long and that the test series as a whole was too protracted as well. The fixed nature of the pressure series, while reducing the chance that larvae would be overstimulated if initially exposed to higher pressure changes, confounded possible differences in response to different pressure changes with habituation to the stimulus or possible learning effects. A second series of experiments was designed therefore to reduce or eliminate some of these problems.

EXPERIMENT II

Design

The major features of the second design were: 1) a single factor, developmental stage of the bulla system; 2) all herring tested individually; 3) an independently randomized test sequence for each fish; 4) each pressure change tested twice; 5) shorter duration of the test series (Fig. 1b) (the larvae were subjected to 23 changes of pressure rather than 47 as in the first experiment); and 6) experiments started when herring were at the center of the test column. Eleven herring of each developmental stage were tested.

TABLE 3.—Analysis of variance of the number of compensatory responses of herring in the second experiment and table of means: I = bulla absent, II = bulla liquid filled, III = bulla gas filled.

Source	df	Mean square	F
Developmental stage	2	62.9394	5.86**
I versus II	1	0.4091	0.030
I and II versus III	1	125.4697	11.68**
Experimental error	30	10.7394	

Average number of compensatory responses per fish:

Stage I	14.18 (62%)
Stage II	13.91 (60%)
Stage III	18.18 (79%)

**$P<0.01$.

Results

As in the first experiment, average positions within the test cylinder were calculated for each pressure change. Vertical movements, as indicated by successive differences in these averages, were then scored as compensatory, anticompensatory, or no response. Analysis of variance of the number of scores indicated that herring with gas-filled bullas compensated more frequently than herring having either liquid-filled bullas or no bullas at all (Table 3; Fig. 4). The stage-III herring on the average moved vertically to compensate 79% of the time compared with 60% and 62% for stage-II and stage-I herring, respectively. However, in Figure 4 we show that even several stage-I larvae achieved relatively high scores, suggesting that a different test of the hypothesis might be based upon classifying larvae into two

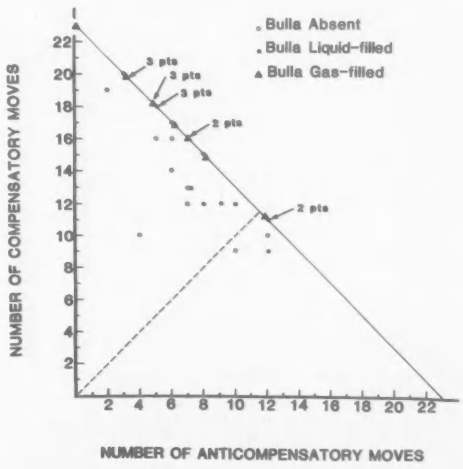

FIGURE 4.—Total numbers of compensatory vertical movements by individual herring in Experiment II plotted against the number of anticompensatory moves. (See legend for Fig. 2.)

categories: 1) those that made more compensatory movements than one would expect by chance, and 2) those that did not.

In Experiment II, each herring was exposed to a random sequence of 23 changes in pressure. If we regard nonresponse as noncompensatory, then the binomial distribution provides a basis for classifying the larvae into two groups, those that moved in the compensatory direction more frequently than one would expect by chance, and those that did not. Under the null hypothesis the probability that a herring would make 16 or more compensatory shifts in vertical position is <0.05. Using this criterion, we classified 5 of the stage-I larvae, 4 of the stage-II larvae, and 10 of the stage-III larvae as having made more compensatory vertical movements than one would expect by chance. A chi-square test showed that the stage-III larvae more frequently compensated for the imposed pressure change than the two earlier stages (chi-square = 7.69, df = 2, $P<0.03$). This implies that the bulla system contributes to the larval herring's hydrostatic pressure perception only after it contains gas.

Because the average position of a larval herring was determined for each pressure level, we could calculate the average vertical distance it moved for each change in pressure. The average distances moved for the 19 successful fish were regressed against the corresponding change in pressure (Fig. 5). The lines for stage-I and stage-II larvae nearly coincide and their slopes are about half that of the regression for stage-III herring. The greatest departure from these lines, fitted through the origin, is for the stage-III herring at the -66 cm H_2O ΔP. They failed to move downward in the column as much as their performance at other pressure changes would predict. We note that even the stage-III herring moved only about 17% of the distance required to compensate fully for an imposed pressure change.

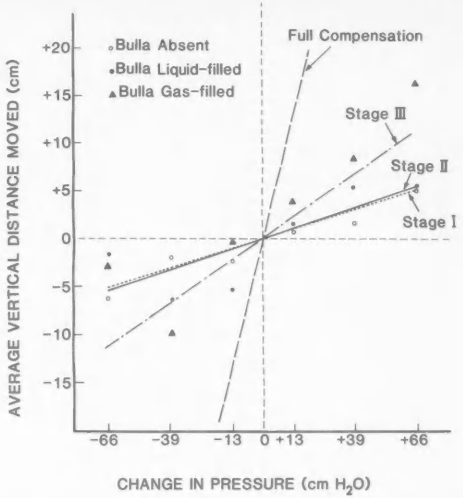

FIGURE 5.—Average vertical distances moved by herring larvae to compensate for changes in pressure.

Discussion

The average proportion of tests in which a larval herring moved vertically to compensate was higher in the second experiment than in the first. This was probably due to the shorter duration of the trials and the test series which should have reduced any effects of habituation or fatigue. However, the random nature of the pressure changes in the second experiment may also have contributed to the enhancement of the response.

Both of the experimental designs employed in this investigation yielded information. The first design revealed that when two herring are tested simultaneously, the response of each is influenced by the presence of the other. It also revealed that the response of a herring to a repeated pressure change tends to increase and then decrease over a 20-min period. The second design provided a more satisfactory test of the null hypothesis that a herring's response to pressure change is independent of the developmental stage of the bulla system and also confirmed an implication from the first experiment: namely, that even before the full development of the bulla system, herring are capable of detecting changes in pressure of the magnitude used in this investigation. Finally, the second experiment demonstrated that herring possessing a gas-filled bulla system will exhibit a markedly improved performance when compared with less mature larvae.

In very few instances did the larvae move a sufficient vertical distance to fully compensate for the imposed pressure change—a similar finding to that of Blaxter and Denton (1976). Even the stage-III larvae, on the average, only moved 17% of the distance to compensate fully. This is partly a statistical artifact of the manner in which we measured a larva's response. We re-

corded its position at 15-s intervals over the 2.5-min period of a given ΔP and then averaged those 10 values. Thus, unless a larva either overcompensated or fully compensated during the first 15 s, its average position during the 2.5-min test would necessarily not be at the level of compensation.

The vertical and horizontal limits of the apparatus also probably impeded vertical progress of larvae in some instances, because the position of the larva within the apparatus at the initiation of a change in pressure determined the potential vertical distance the larva could move to compensate; this would be most important as a source of bias at the larger ΔP's.

Still another possible explanation for the incomplete nature of the compensation may lie in the artificiality of the experiment. Fish are not normally subjected to abrupt hydrostatic pressure changes as they swim with a vertical component. It is difficult to design an experiment to show a hydrostatic pressure sense in a free swimming vertically moving fish larva. Gibson[5] has shown, however, that the activity of juvenile plaice (which lack a swim bladder) varies regularly during sinusoidal changes of hydrostatic pressure of amplitudes of about 50 cm H_2O repeated over a 4-h period, thus demonstrating sensitivity to slow changes of pressure in a fish without a swim bladder.

The site of pressure sensitivity in the herring larvae has not been identified, but it seems to be related to the bulla because sensitivity is enhanced when the bulla is full of gas. It is possible that abrupt changes of pressure applied to the top of a column of water might generate particle displacements in the water that could be perceived by neuromast organs. We do not believe this is a likely explanation of the observed pressure sensitivity in stage-I and stage-II larvae, however, because in some experiments the pressure change was applied over about 5 s, which reduced any resonant effects in the apparatus, but was equally successful in causing correct responses.

Because the swim bladder serves as a gas reservoir for the bulla, the bulla cannot provide perception of absolute pressure for a juvenile or an adult herring. However, in the larva the development of the gas-filled bulla precedes that of the swim bladder and therefore the bulla may temporarily serve as a depth indicator (Blaxter et al. 1981), permitting a larva to limit the maximum depth reached during vertical movements initiated by changes in light intensity. Having a mechanism to limit the maximum depth of vertical migration may enable a larva to maintain its position in the water column. This could be of adaptive value similar to that described for anchovy by Hunter and Sanchez (1976), in that it may serve to keep larvae together and facilitate the development of schooling. A depth indicator might also serve as an energy-saving mechanism if it enables a larva to maintain its position in that portion of the water column where food is most abundant.

In conclusion, we have found that herring larvae display pressure sensitivity both before and after the bulla system has developed, although it is enhanced in larvae with a gas-filled bulla. The threshold of sensitivity was not determined but lies below 13 cm H_2O (1 cm Hg). For a herring larva near the sea surface this observation implies that pressure sensitivity is $<1.3\%$ of the ambient pressure. Prior treatment of larvae to 5 atm pressure did not significantly impair sensitivity.

[5]R. N. Gibson, Principal Scientific Officer, Dunstaffnage Marine Research Laboratory, P.O. Box No. 3, Oban, PA34 4AD, Argyll, Scotland, pers. commun. March 1979.

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FEEDING ECOLOGY OF SOME FISHES OF THE ANTARCTIC PENINSULA[1]

ROBERT A. DANIELS[2]

ABSTRACT

Feeding ecology of 19 species of Antarctic fishes is examined. All species are carnivorous; the most important prey are amphipods, polychaetes, and isopods. Seven of the species examined (*Notothenia neglecta, N. gibberifrons, N. nudifrons, N. larseni, N. kempi, Trematomus scotti,* and *T. bernacchii*) are feeding generalists with diets varying with size of fish, season, and locality of capture. Seven other species (*Trematomus newnesi, Pleuragramma antarcticum, Cryothenia peninsulae, Artedidraco skottsbergi, Harpagifer bispinis, Prionodraco evansii,* and *Parachaenichthys charcoti*) are specialists, feeding predominantly upon prey either from a single taxon or from very few taxa. Five species (*Notothenia rossii, Trematomus eulepidotus, Cryodraco antarcticus, Pagetopsis macropterus,* and *Chaenocephalus aceratus*) were not well represented in the samples, but a qualitative description of their diet is included. The fishes studied consume a wide variety of food types and use several feeding behaviors. Based on field and laboratory observations, most species are ambush predators. However some species use an indiscriminant slurp method, grazing, or a search and capture form of feeding. Some species switch feeding behaviors seasonally or with locality. Diet similarity is high only in morphologically similar species. Where a high degree of diet similarity occurs, overlap in distribution tends to be low. Although most species are high-level carnivores and at least some occur sympatrically, direct competition for food among the species does not appear to exist. This partitioning of food resources adds to the complexity of the structure of Antarctic communities. The position of these fishes in the Antarctic trophic structure should be further examined and considered before extensive exploitation is begun.

Feeding ecology in Antarctic fishes has, until recently, attracted little attention. Richardson (1975) described the diets of four species of fish found along the Antarctic Peninsula and discussed diet overlap. In a thorough study, Targett (1981) examined the trophic structure of five demersal fish communities off Antarctic and sub-Antarctic islands. Permitin and Tarverdiyeva (1972, 1978) examined degree of diet similarity among 10 fishes from the sub-Antarctic island, South Georgia, and in nototheniids and channichthyids collected from the South Orkney Islands, an archipelago north of the Antarctic Peninsula. Moreno and Osorio (1977) examined diet changes with depth in one species, and Wyanski and Targett (1981) reported on diets of nine harpagiferids. Others (Arnaud and Hureau 1966; Holloway 1969; Arnaud 1970; Hureau 1970; Everson 1970; Permitin 1970; Meier 1971; Yukov 1971; DeWitt and Hopkins 1977; Moreno and Zamorano 1980; Duarte and Moreno 1981) described one component of the diet of various fishes, the diet of one species or qualitative descriptions of stomach contents. This study examines several aspects of feeding ecology of Antarctic fishes, including seasonal, spatial, and size-related changes. With increasing interest in the exploitation of Antarctic resources (Lyubimova et al. 1973), the need to understand the feeding ecology of these fishes and their position in Antarctic communities has become important.

STUDY AREA

The Antarctic Peninsula reaches north from the continent to lat. 63°18′S, long. 55°02′W. Its west coast is flanked by numerous islands which create many bays, inlets, straits, and small coves. Weather conditions and longevity and distribution of fast and brash ice vary along the peninsula seasonally, yearly, and with area. Water temperatures at Palmer Station (lat. 64°46′S, long. 64°04′W) fluctuate approximately 2°C from 0°C; salinities range from 32.2‰ to 33.5‰ except immediate to shore and in surface waters during the spring thaw; dissolved oxygen remains near saturation at 6-10 cc/l; pH ranges from 7.9 to 8.5 (Krebs 1974; Showers et al. 1977). Primary productivity varies greatly along the peninsula (Krebs 1974) and in the Antarctic in

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general (El-Sayed 1968) through the year. The composition of the sea bed varies among mud, rubble, and bedrock. Mud bottoms, consisting of glacial flour and diatomaceous oozes, are most common and are found in most straits, bays, and large inlets. Rubble bottoms, composed of heterogeneous mixtures of gravel, cobbles, and boulders, are generally found in small, protected, nearshore coves. Rock cliffs are common along coastal areas and on many submerged mounts. Each bottom type supports a distinctive fauna (Lowry 1969; DeLaca 1976; Kauffman 1977; Daniels and Lipps 1982). Approximately 40 species of fish are found off the Antarctic Peninsula (DeWitt 1971). Table 1 provides a brief description of the species included in this study.

METHODS

Fish used in this study were collected at 11 sites from Terra Firma Islands, Margurite Bay (lat. 68°42′S, long. 67°32′W) to Low Island (lat. 63°25′S, long. 62°10′W) using otter and Isaacs-Kidd trawls, long lines, barrel nets, mud grabs, and hand nets used by scuba divers between 27 January and 28 December 1975 (Fig. 1). Samples were taken at most sites in February or March; a second collection was taken in December at four sites. In areas adjacent to Palmer Station, fish were collected at monthly intervals from January to December.

Fish were preserved immediately in 4% buffered formaldehyde solution; preservative was injected into the stomach cavities of larger specimens. Most species did not regurgitate stomach contents when placed in preservative. However, most channichthyids everted their stomachs when caught; therefore, these species are not included in the analysis and only a qualitative description of their diets is presented. A total of 1,609 stomachs of 19 species were examined. Each of the major Antarctic families is represented: 12 nototheniids, 2 harpagiferids, 2 bathydraconids, and 3 channichthyids. Specimens were later measured (standard length

TABLE 1.—Distribution and morphometric data of fishes collected off the Antarctic Peninsula, 1975. Information on ranges from Norman (1940) and DeWitt (1971).

Species	Distribution	Probable habitat	Relative abundance in samples	Basic body shape	Adult size range (SL mm)	Position of mouth
Nototheniidae						
Notothenia neglecta	circumpolar	rubble-algae	common	bullheadlike	200-300	terminal
Notothenia gibberifrons	Antarctic Pen. South Georgia Scotia Ridge	mud	abundant	bullheadlike	200-300	subterminal
Notothenia nudifrons	Antarctic Pen. South Georgia Scotia Ridge	rocky cliff, mud	abundant	fusiform	100-150	terminal
Notothenia larseni	Antarctic Pen. South Georgia Scotia Ridge	column, bentho-pelagic	abundant	fusiform	100-150	terminal
Notothenia rossii	circumpolar	rubble-algae	rare	bullheadlike	200-300	terminal
Notothenia kempi	Antarctic Pen.	pelagic, bentho-pelagic	rare	fusiform	150-300	slightly supraterminal
Trematomus scotti	circumpolar	pelagic, bentho-pelagic	abundant	fusiform	100-150	terminal
Trematomus newnesi	circumpolar	pelagic, bentho-pelagic	common	fusiform	150-200	supraterminal
Trematomus bernacchii	circumpolar	rubble-algae	common	bullheadlike	150-250	terminal
Trematomus eulepidotus	circumpolar	rubble-mud	rare	fusiform	150-250	supraterminal
Pleuragramma antarcticum	circumpolar	pelagic	common	fusiform	100-150	supraterminal
Cryothenia peninsulae	Antarctic Pen.	pelagic	rare	fusiform	100-150	slightly supraterminal
Harpagiferidae						
Artedidraco skottsbergi	circumpolar	mud	rare	bullheadlike	75-100	terminal
Harpagifer bispinis	Antarctic Pen. South Georgia Falkland Is.	rubble-algae	common	bullheadlike	75-100	terminal
Bathydraconidae						
Prionodraco evansii	circumpolar	mud	rare	wedgelike	100-125	terminal
Parachaenichthys charcoti	Antarctic Pen. Scotia Ridge	rubble-algae	rare	wedgelike	200-250	terminal
Channichthyidae						
Cryodraco antarcticus	circumpolar	pelagic	rare	wedgelike	100-150	terminal
Pagetopsis macropterus	circumpolar	pelagic	rare	wedgelike	100-150	terminal
Chaenocephalus aceratus	Antarctic Pen. South Georgia Scotia Ridge	mud	rare	wedgelike	200-300	terminal

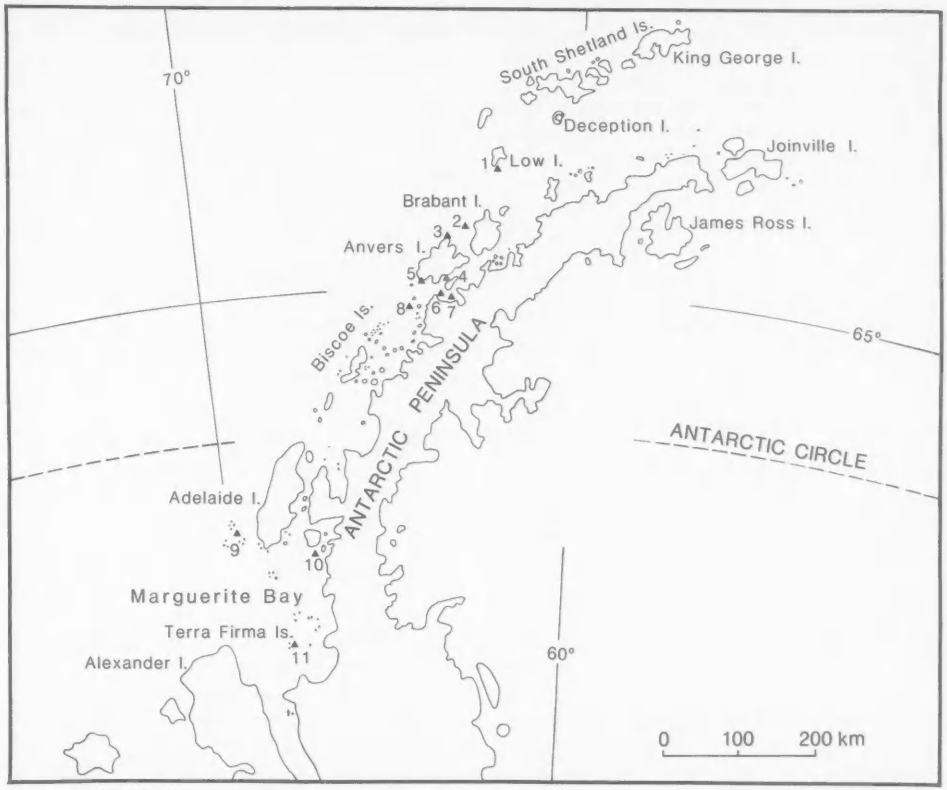

FIGURE 1.—Antarctic Peninsula showing sites where major collections of fish were made, 1975: Low Island (1), Dallmann Bay (2), The Sound, Melchior Islands (3), Port Lockroy (4), Arthur Harbor, site of Palmer Station (5), Peltier Channel (6), Paradise Harbor (7), Argentine Islands (8), Adelaide Island (9), Square Bay (10), and Terra Firma Islands (11).

(SL)), weighed, and dissected. Stomachs were removed, opened, and all contents flushed onto petri dishes. Prey items were sorted, counted, and assigned a point volume (Hynes 1950). One point is approximately equivalent to an isopod *Munna* sp. with an approximate volume of 0.25 ml and approximate dimensions of $15 \times 5 \times 3$ mm; one point was also approximately equivalent to 2 mg dry weight. To test the accuracy of the estimated volumes, the contents of 60 stomachs of *Harpagifer bispinis* were assigned a point volume, volume was measured by displacement, and the contents were dried and weighed. There was little difference between the three measurements (Friedman's Test, $0.2<P<0.3$) (Langley 1970). Individual pieces of algae were not counted and were excluded from all calculations involving number of prey items consumed.

The feeding and foraging behavior of eight species were observed in tanks at Palmer Station and on 140 scuba dives. Twenty-two dives were specifically planned to observe feeding and foraging behavior. In the laboratory, observations were made on recently collected fishes which were introduced into a small cage in a tank where several species of invertebrates were established. The tanks had a gravel substrate, larger rocks, and algae. Invertebrates included in the tanks were scaleworms (*Harmothoe spinosa*), amphipods (*Bovallia gigantea*, *Eurymera monticulosa*), isopods (*Serolis polita*, *Munna* sp., *Cymodocea antarctica*), molluscs (*Patinigera polaris*, *Margarella antarctica*, *Trophon* sp., *Neobuccinum eatoni*), and echinoderms (*Stere-*

chinus neumayeri, Odontaster validus). After a suitable acclimation period (24-48 h), the fish or fishes were released and allowed to feed. Observations were made from above and provided information on feeding method. Foraging strategy is inferred from the feeding method, morphology, and diet of the fish and microhabitat in which it was captured or observed.

Percentage frequency of occurrence of each prey taxon and percentage composition of diet by number and point volume were calculated for each species. Hoffman (1978) suggested a method for determining an adequate sample size in feeding studies. Using this method, three samples containing 35 individuals of each of four species were examined. No additional information was obtained in sample sizes >9-23 individuals ($\bar{x} = 17$). Where possible, at least 20 individuals were examined. When a sufficient number of specimens was collected, the sample was segregated by size of fish, season, or area of capture. These subsamples were then compared using a χ^2 test for association (Remington and Schork 1970). Fullness indices, measures of feeding intensity (Windell 1971), were calculated for each subsample, and significance was determined by Wilcoxon sum of ranks test (paired samples) or Kruskal-Wallis χ^2 test (3 or more samples) (Langley 1970). Mean prey size was calculated by dividing total volume per taxon by total number of prey items consumed. Percentage diet similarity by number and volume was determined using:

$$S = 100\,(1 - \tfrac{1}{2}\ \textstyle\sum_i |p_{xi} - p_{yi}|)$$

where p_{xi} and p_{yi} are the proportions of the diets of species x and y respectively of prey item i (Linton et al. 1981; Abrams 1980; Schoener 1970). Diet diversity was examined by the number of taxa found in the diet of each species (P) and diversity index $H = -\Sigma p_i \ln(p_i)$, where p_i = the proportion of the ith species in the sample (Shannon and Weaver 1949).

RESULTS

Feeding Behaviors

Fishes were observed using variations of four basic behaviors: ambush feeding, bottom slurping, water column feeding, and grazing. Ambush feeding was observed most frequently in the field. *Harpagifer bispinis, Notothenia neglecta, Trematomus bernacchii* usually, and *N. gibberifrons*, on occasion, perched among rocks or partially buried themselves in soft mud and waited for a prey organism to approach. As the prey neared, the fish lunged and then engulfed the item. Treatment of the prey after capture depended upon its relative size and morphology. If possible, the item was swallowed whole. Exceptions to this were scaleworms. In the laboratory, I observed *H. bispinis* capture a scaleworm on 16 occasions, pull it into its mouth, spit it out, immediately pull it into its mouth again, and repeat the process several more times ($\bar{x} = 6$, range = 2-16). This procedure successfully removed all scales from the worm before the fish actually consumed it. This process apparently occurred in the wild since scales are rarely found in *H. bispinis* stomachs although scaleworms are an important part of its diet (below). If the prey item was too large to engulf whole, it was eaten in parts. I observed *N. neglecta* capturing fish one-third to one-half as long as itself on five occasions in laboratory tanks. The predatory *N. neglecta* pulled the prey fish *T. bernacchii* or *N. nudifrons* into its mouth, usually head first, retreated to a protected area, and began to digest that part of the fish in its mouth and stomach. This process took up to 12 h during which time the predator was quiescent. Large prey items taken from the stomachs of *N. neglecta* commonly showed signs of differential digestion, which indicates that this method of feeding occurs in the wild. Fish using ambush feeding tended to be largely carnivorous and preyed upon relatively large, motile organisms. Fishes were observed to take only moving organisms. On many occasions in the laboratory, *H. bispinis* ignored stationary amphipods close to its mouth and readily visible. When the amphipod moved, it was consumed. Often movement consisted only of a twitching antenna.

The slurp feeding method was observed most frequently in *N. gibberifrons* which swam over mud bottoms, sucked up and sifted through large quantities of mud, and consumed the organisms encountered (Daniels and Lipps 1978). Mud and small rocks were also swallowed and passed through the gut. Fish using this method usually fed upon sedentary or slow-moving invertebrates and rarely consumed plant matter. Bacteria adherent to mud may also have been an important part of their diet.

Water column feeding was characteristic of the pelagic *P. antarcticum*, juvenile *T. newnesi*, and, on occasion, demersal forms like *N. neglecta*.

Pleuragramma antarcticum was observed under fast ice in schools of several thousand individuals on three occasions. Individuals darted about and frequently approached the ice-water interface where they appeared to bite at and consume small amphipods (*Nototropis* sp.). Individual juvenile *T. newnesi* also entered the water column under an ice cover or during other periods of low light intensity. These fish generally were found in shallow-water brown algae, *Desmeristia anceps*, beds except when ice was present and light conditions were favorable. They then left the beds individually and occupied the water column where they fed on the undersurface of the ice, or the substrate or in the column. On one occasion, one large *N. neglecta* (400 mm SL) entered the water column and ate several *P. antarcticum* from a school before returning to a rock outcropping. Fishes using this feeding method usually fed upon motile invertebrates, such as eupausiids, pteropods, and amphipods, or other fishes often associated with the pelagic or cryopelagic communities.

Grazing, although never observed, appeared to be an important feeding method in some species, most notably *N. neglecta*, during spring and summer. Individuals were collected with large sheets of macroalgae (e.g., *Phyllogigas grandifolius*, *Iridaea obovata*, or *Desmeristia* spp.), solitary, epiphytic diatoms (*Trigonium acticum*, *Cocconeis imperatrix*, *Amphora* sp., *Grammatophora* sp., *Licmophora* sp., and *Achnanthes* sp.), and epibenthic diatoms (*Biddulphia anthropomorpha*, *Melosira sol*, *Amphora* sp., *Grammatophora* sp., *Licmophora* sp., *Achnanthes* sp., and *Isthmia* sp.) in their stomachs.

It was inferred from stomach contents that fishes commonly switched from one feeding method and/or foraging area to another with season. *Notothenia neglecta* ambushed prey from rock outcroppings and algae beds through much of the year. During the spring and summer plankton blooms, however, some individuals began to search for food on homogeneous mud bottoms away from any protective rock crannies, as evidenced by large numbers of mud-bottom isopod *Serolis polita* in some stomachs in December. During spring and summer, individual *N. neglecta* cropped macroalgae and harvested diatom mats from mud and gravel bottoms. *Notothenia gibberifrons* used the slurp feeding method to forage in more northern areas but ambushed its prey in southern areas (Daniels and Lipps 1978).

Diets

Diets varied among the 14 species examined so that fishes could be ranked from specialized feeders to feeding generalists (Tables 2, 3, 4). Seven species were generalists (high P and H) and seven species were specialists (low P and H). Generalists consumed a variety of organisms which were phylogeneticly and morphologically distinct. Specialists preyed upon organisms with similar morphologies or in the same prey taxon. There appeared to be two types of specialists: in one group, *Cryothenia peninsulae*, *Harpagifer bispinis*, *Artedidraco skottsbergi*, and *Parachaenichthys charcoti*, the diet consisted largely of organisms from one prey taxon; while in the second, *Trematomus newnesi*, *Pleuragramma antarcticum*, and *Prionodraco evansii*, relatively few prey taxa were consumed in approximately equal numbers. Although quantitative data on food availability were not collected, generalists also appeared to be feeding opportunists that ate the most abundant available prey. Individuals in the generalist species also tended to be generalists. Individual *N. neglecta* commonly consumed prey from 5 to 10 taxa (87% of sample) and most of the available prey in the algae beds of Arthur Harbor (Lowry 1969) were found in stomachs of *N. neglecta*. Specialists tended to be more selective. In the rubble bottom community where *H. bispinis* was collected, gastropods, small echinoderms, and errant polychaetes were abundant, yet, except for the scaleworms, which became seasonally important, were rarely found in *H. bispinis* stomachs. Individuals in the specialist species also tended to be specialists; 91% of the *H. bispinis* examined had consumed prey from one or two taxa.

Amphipods were the prey item most fequently taken by fish (Tables 2, 3, 4). However, they were the most important component by volume in only *H. bispinis* and *A. skottsbergi*. Polychaetes were also frequently consumed and were an important part of the diet of *N. nudifrons*, *N. larseni*, *T. scotti*, and *A. skottsbergi* by both number and volume. Isopods, gastropods, and pelecypods also occurred consistently, but were relatively minor components in most diets. Other taxa were important dietary items for only particular species or at particular times of year. Euphausiids, *Euphausia superba* and *E. chrystallorophias*, dominated the diets of *N. larseni*, *T. scotti*, *T. newnesi*, *T. bernacchii*, *Pleuragramma antarcticum*, and *C. peninsulae* by number and volume.

TABLE 2.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (*P*) and diversity index (*H*) of fishes of the genus *Notothenia* collected off Antarctic Peninsula, 1975. See text for explanation of terms.

	N. neglecta			*N. gibberifrons*			*N. nudifrons*			*N. larseni*			*N. kempi*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.
Number examined		173			339			164			278			18	
Foraminifera	<1	<1	<1	2	4	<1	<1	<1	<1	4	2	<1	6	2	1
Porifera	<1	<1	<1	4	<1	<1									
Coelenterata	<1	<1	<1	<1	<1	<1				<1	<1	<1			
Ctenophora	2	<1	<1							<1	<1	<1			
Nemertea	10	<1	6	4	<1	1	<1	<1	<1	<1	<1	1			
Nematoda				7	1	<1	3	1	<1						
Bryozoa	1	<1	<1	<1	<1	<1									
Brachiopoda				<1	<1	<1									
Oligochaeta				<1	<1	<1									
Polychaeta, sedentary				65	21	27									
errant	21	<1	2	21	2	9	43	22	45	18	10	12	44	19	31
Mollusca															
Gastropoda	75	10	4	15	2	1	12	4	3	1	<1	<1	11	7	4
Pelecypoda	6	<1	<1	38	8	6	1	<1	<1	<1	<1	<1			
Scaphopoda				3	<1	<1									
Cephalopoda	1	<1	<1	<1	<1	<1				<1	<1	<1			
Arthropoda															
Crustacea															
Amphipoda	94	84	21	54	51	19	66	56	31	39	36	12	22	25	17
Isopoda	15	1	7	7	1	3	23	8	7	5	3	1	28	25	20
Cumacea				9	2	1	1	<1	<1	3	3	<1	17	7	8
Euphausiacea	6	<1	4	6	<1	5	2	<1	1	30	27	54	11	4	9
Ostracoda	3	<1	<1	7	<1	<1	7	2	<1	<1	<1	<1			
Copepoda	15	1	<1	3	<1	<1	1	<1	<1				17	9	4
Pycnogonida	1	<1	<1	2	<1	5	7	2	4	<1	<1	<1			
Echinodermata															
Asteroidea										<1	<1	<1			
Echinoidea	<1	<1	<1	<1	<1	<1	<1	<1	<1						
Holothurioidea	3	<1	<1	1	<1	1									
Crinoidea				1	<1	<1	4	1	5	<1	<1	<1			
Ophiuroidea				9	2	8	<1	<1	<1	1	<1	<1			
Chordata															
Tunicata	<1	<1	<1	2	<1	1	1	<1	<1	3	<1	<1	6	2	1
Pisces	13	<1	28	<1	<1	3				1	2	2			
Egg mass	3	1	1							2	3	7			
Macroalgae	80		21	12		2	3		<1	3		1			
Diatoms	12		3												
Miscellaneous			<1			3			<1			2			5
Taxa (*P*)		24			28			18			22			9	
Diversity (*H*)		1.99			2.31			1.53			1.61			1.88	

Fish are a major part of the diet of *N. neglecta* and *Parachaenichthys charcoti* by volume but were unimportant by number.

Changes with Locality

In *N. gibberifrons*, *N. larseni*, *T. scotti*, and *H. bispinis*, the diets of individuals of a similar size group caught at the same time of year but in different localities showed significant differences in the prey taken (Fig. 2) and in the amount of food consumed (Table 5). In each species, approximately the same number of prey taxa were consumed, but only in *H. bispinis* were the taxa identical. The other species consumed not only different amounts from each taxa, but also different types of prey. This change in diet is most dramatic in *N. gibberifrons* (Fig. 2). Individuals from the more northerly Peltier Channel tended to consume sedentary invertebrates such as sedentary annelids, clams, and cumaceans which are often found buried up to several centimeters in the mud. Individuals from the samples of the southern Terra Firma Islands tended to consume motile, rubble-bottom organisms, such as errant polychaetes, amphipods, and fish.

Ontogenetic Changes

Sample sizes were large enough in six species to compare differences in diet with fish size. Within each species, individuals collected from the same locality at the same time but of different size tended to consume prey from the same taxa, but the relative importance of each taxon by volume varied significantly (χ^2, $P<0.02$) (Figs. 3, 4). In all species mean prey size, mean number of prey items consumed, and number of different prey types consumed increased with fish size. Diet diversity showed no size-related change in any species except in *T. bernacchii* (Table 6).

TABLE 3.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (*P*) and diversity index (*H*) of fishes of the genera *Trematomus*, *Pleuragramma*, and *Cryothenia* collected off Antarctic Peninsula, 1975. See text for explanation of terms.

	T. scotti			*T. newnesi*			*T. bernacchii*			*P. antarcticum*			*C. peninsulae*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.
Number examined		146			37			76			17			18	
Foraminifera										3	13	2			
Coelenterata	<1	<1	<1												
Nemertea	5	2	2				12	<1	23						
Nematoda	2	<1	<1												
Brachiopoda	<1	<1	1												
Polychaeta, sedentary	23	29	16				4	<1	4				17	6	4
errant	36	14	18	11	6	6	22	2	10	3	2	2	6	1	<1
Mollusca															
Gastropoda	4	2	1	6	3	1	12	1	4						
Pelecypoda	8	3	<1				3	<1	<1						
Arthropoda															
Crustacea															
Amphipoda	29	19	6	47	33	23	72	89	26	7	5	2	6	1	<1
Isopoda	4	3	<1	6	3	1	18	3	12						
Cumacea	7	5	<1							33	53	10			
Euphausiacea	35	13	48	35	53	68	8	4	2	40	24	69	100	92	95
Ostracoda	<1	<1	<1				1	<1	<1						
Copepoda							1	<1	<1						
Pycnogonida	3	1	1				1	<1	<1						
Echinodermata															
Holothurioidea	<1	<1	<1												
Crinoidea	<1	<1	<1												
Ophiuroidea	4	2	1												
Chordata															
Tunicata	1	<1	<1				1	<1	3						
Pisces							1	<1	<1	7	3	3			
Egg mass	<1	1	<1												
Macroalgae	2		1				16		3						
Miscellaneous			2						12						
Taxa (*P*)		20			5			14			6			4	
Diversity (*H*)		1.60			0.84			1.97			0.79			0.33	

TABLE 4.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (*P*) and diversity index (*H*) of harpagiferids and bathydraconids collected off the Antarctic Peninsula, 1975. See text for explanation of terms.

	Artedidraco scotsbergi			*Harpagifer bispinis*			*Prionodraco evansii*			*Parachaenichthys charcoti*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.
Number examined		17			237			21			12	
Foraminifera	6	3	<1									
Polychaeta, errant	47	25	47	27	4	16	28	7	19			
Mollusca												
Gastropoda				4	<1	<1						
Pelecypoda				1	<1	<1						
Arthropoda												
Crustacea												
Amphipoda	59	61	46	88	88	79	24	19	29	38	72	8
Isopoda	12	10	5	24	5	4						
Cumacea							38	65	31			
Euphausiacea							19	8	21	50	22	15
Ostracoda				2	<1	<1						
Pisces										25	6	76
Egg mass				6	1	<1						
Macroalgae				8		<1				13		1
Taxa (*P*)		4			8			4			4	
Diversity (*H*)		0.88			0.68			1.53			0.72	

Seasonal Changes

Changes in diet in *N. neglecta* and *H. bispinis* were monitored at monthly intervals in Arthur Harbor through the year. *Notothenia neglecta* showed a significant seasonal diet change ($\chi^2 = 727$, df = 104, $P<0.01$); these fishes switched from being omnivores in the austral spring and summer to a carnivorous diet through autumn and winter. *Notothenia neglecta* also consumed a large variety of organisms, including individuals from several different microhabitats such as isopod *Serolis polita* and nemertean worm *Lineas corrugatus* from mud bottom areas,

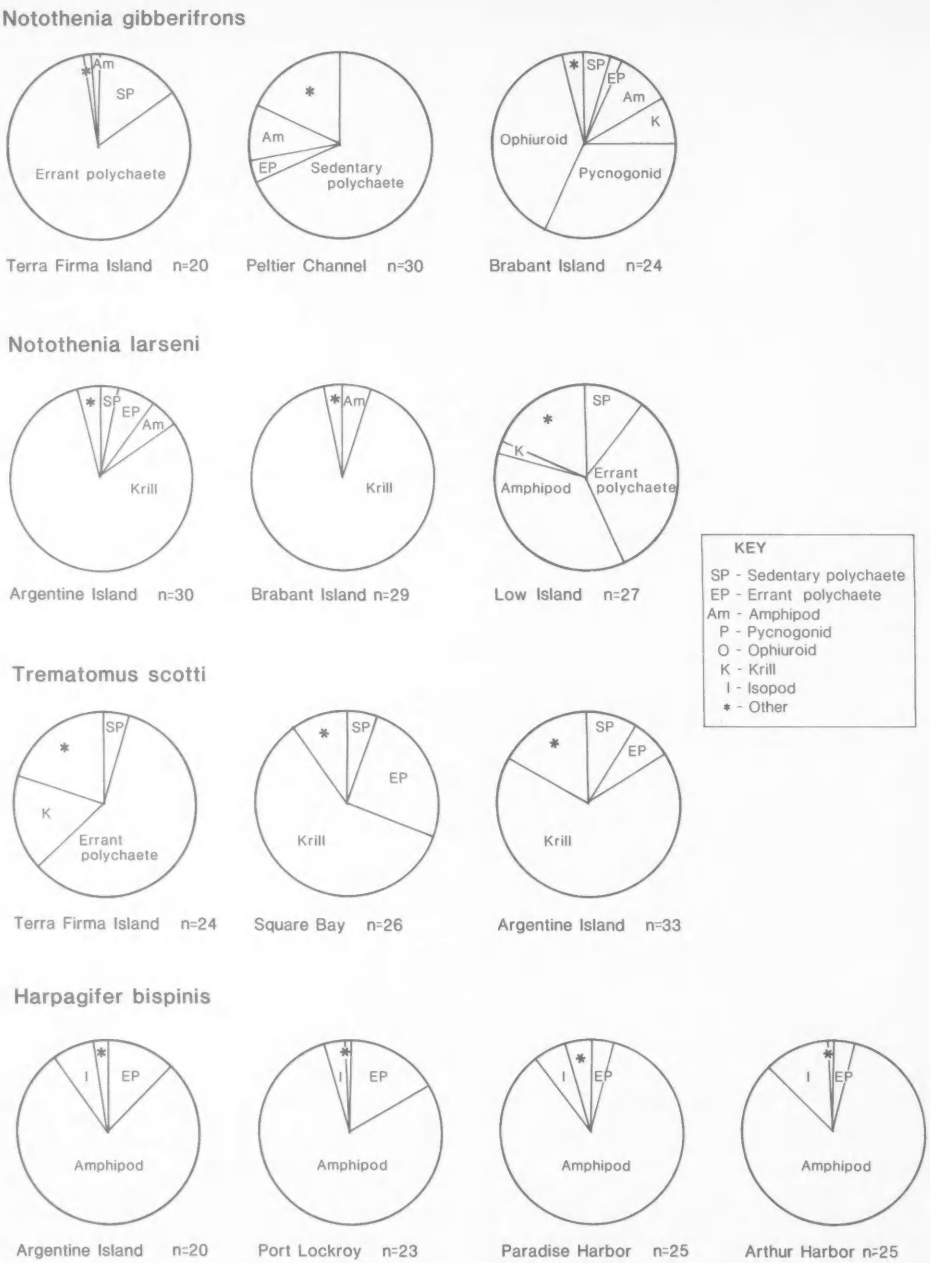

FIGURE 2.—Changes in feeding associated with locality of capture in four notothenioid fishes. Fishes used in comparisons are similar in size and were taken during the same season.

TABLE 5.—Changes in diet by locality of capture in fishes of similar size and taken during the same season off the Antarctic Peninsula, 1975. A χ^2 test for association was used to examine changes in the volume of each taxon consumed; a Kruskal-Willas χ^2 test was used to examine changes in feeding intensity (fullness index).

Species	Area	*n*	SL (mm)	Range (mm)	No. taxa consumed	Volume		Fullness index		
						χ^2	*P*	$\bar{X}$	χ^2	*P*
Notothenia gibberifrons	Peltier Chan.	30	146	106-217	13			6.8		
	Terra Firma Is.	20	123	100-146	13			8.2		
	Brabant I.	24	134	87-260	12	393.1	<0.01	7.5	8.5	<0.05
N. larseni	Brabant I.	29	120	70-150	4			8.1		
	Low I.	27	114	84-152	8			6.6		
	Argentine Is.	30	113	72-162	10	224.6	<0.01	2.4	20.2	<0.01
Trematomus scotti	Terra Firma Is.	24	69	45-90	7			7.0		
	Square Bay	26	98	61-137	9			4.9		
	Argentine Is.	33	99	63-126	15	104.9	<0.01	6.9	15.8	<0.01
Harpagifer bispinis	Argentine Is.	20	71	58-80	6			4.4		
	Port Lockroy	23	67	43-82	5			8.4		
	Paradise Harbor	25	68	57-88	5			5.5		
	Arthur Harbor	25	70	51-85	5	42.1	<0.01	8.2	14.1	<0.01

TABLE 6.—Size-related changes in diet in Antarctic fishes, Antarctic Peninsula, 1975. Fish in each species were collected at the same time from the same locality.

Species	Capture	Size group	*n*	SL $\bar{X}$ (mm)	SL range (mm)	Mean no. items/stomach	Mean prey size (vol./item)	No. taxa consumed	Mean *H*
Notothenia neglecta	Arthur Harbor December	I	10	80	71-90	13.8	0.9	7	0.5
		II	8	199	165-231	82.0	4.5	8	0.8
		III	9	292	258-313	37.0	12.8	12	0.6
Notothenia gibberifrons	Peltier Chan. February	I	14	80	49-99	5.8	0.6	10	0.8
		II	20	129	116-148	8.0	1.2	13	0.8
		III	20	193	163-217	10.9	1.8	15	0.9
Notothenia nudifrons	Dalmann Bay December	I	28	50	32-65	4.7	0.2	10	0.7
		II	16	116	93-153	4.3	0.7	11	0.7
Notothenia larseni	Low I. March	I	16	94	82-105	2.7	1.8	4	0.3
		II	19	139	113-157	2.4	3.7	7	0.5
Trematomus scotti	Argentine Is. March	I	18	84	63-99	3.0	1.6	11	0.5
		II	17	121	108-144	2.7	3.3	13	0.8
Trematomus bernacchii	Arthur Harbor June	I	13	60	60-78	15.0	0.5	4	0.1
		II	14	138	107-160	31.4	2.7	8	0.3
		III	14	200	180-233	10.1	8.1	10	0.7

krill and *Pleuragramma antarcticum* from the pelagic and cryopelagic communities, limpet *Patinigera polaris* from rocky cliffs, and a large number of organisms from rubble-bottom areas, the habitat from which this species was most frequently collected. *Harpagifer bispinis* consumed prey from the same taxa through the sampling period, but the importance of each taxon differed ($\chi^2 = 149$, df = 21, $P<0.01$). The significance results from a midwinter peak in abundance of scaleworms. This species consumed organisms from the rubble-bottom community which consisted largely of the amphipods *Bovallia gigantea*, *Eurymera monticulosa*, the scaleworm *Harmothoe spinosa*, and the isopods, *Munna* sp. and *Cymodocea antarctica*.

Differences in diet of similar-sized individuals of *Notothenia gibberifrons*, *N. nudifrons*, *N. larseni*, and *T. scotti* collected at the same locality at different times of year were significant in the relative importance of each prey taxon, but tended to show no significance in the amount of food consumed (Table 7). In all four species individuals tended to consume prey from the same number of taxa. Spring samples tended to contain individuals of a smaller size than late summer samples.

Dietary Similarity

Diets were >60% similar in 17 species pairs by number and in 11 species pairs by volume (Table 8). Similarity in diet by number of prey items consumed is greater due to the large number of amphipods taken by most fishes. A high percentage similarity by volume, a value more indicative of the importance of each food type, was obtained for morphologically similar species such as the two harpagiferids, *A. scottsbergi* and *Harpagifer bispinis*, and the pelagic-benthopelagic complex of *N. larseni*, *T. scotti*, *T. newnesi*, *Pleuragramma antarcticum*, and *Cryothenia peninsulae*. Species that were generalists showed 30-60% similarity in diet with other

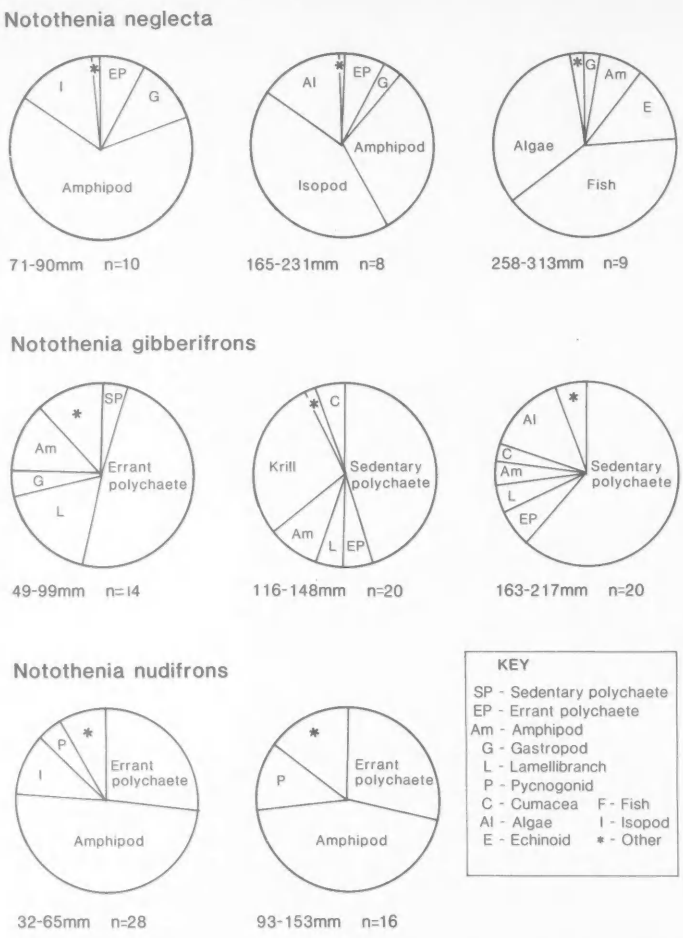

FIGURE 3.—Size-associated changes in feeding in three *Notothenia* spp. collected at the same locality on the same day.

generalists and <30% similarity with the more specialized feeders. Generalists were often collected at sites with other generalists and specialists. The tendency among specialized feeders was one of low percentage similarity in both diet and distribution.

Other Species

Four *N. rossii*, morphologically similar to *N. neglecta*, consumed prey from six taxa. Amphipods were most important by number (81%); krill (31%) and demersal fish (51%) were important by volume. Krill was the most important component by number and volume in the diets of five *T. eulepidotus*, seven *Pagetopsis macropterus*, and eight *Cryodraco antarcticus*. These species consumed prey from relatively few taxa and were exclusively carnivorous. *Trematomus eulepidotus*, morphologically similar to *T. scotti*, in addition to the pelagic krill, also consumed cumaceans which are typically associated with mud bottoms. The channichthyids, *P. macropterus* and *C. antarcticus* also consumed fish, such as

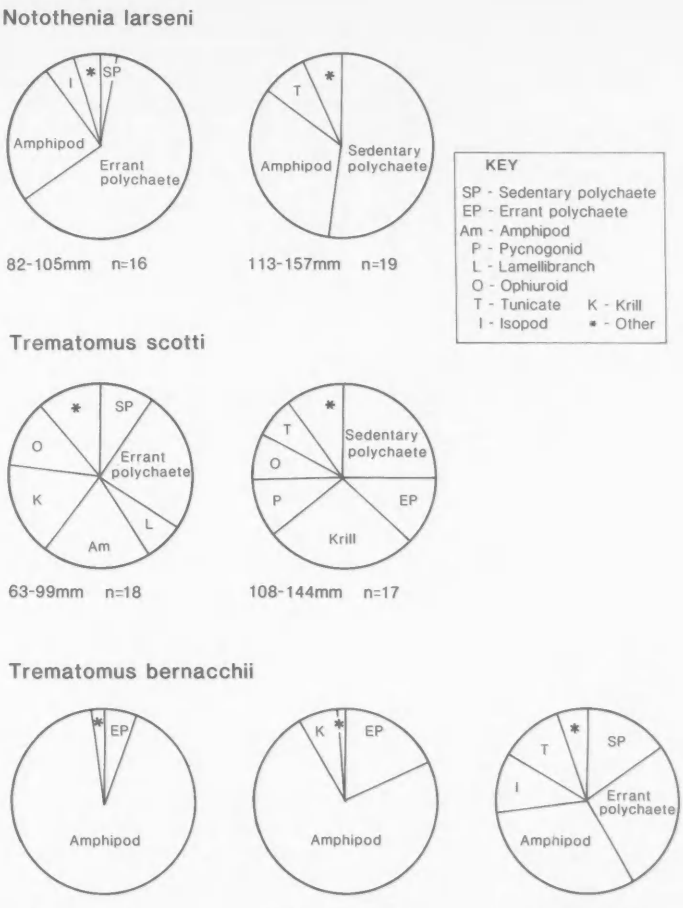

FIGURE 4.—Size-associated changes in feeding in three nototheniids collected at the same locality on the same day.

the pelagic *Pleuragramma antarcticum* and the demersal *N. nudifrons*. In one *Pagetopsis macropterus* collected in Margurite Bay, both species of krill found in the area were present. The stomachs of 42 *Chaenocephalus aceratus* were examined and found to be empty.

DISCUSSION

Antarctic fishes show great variety in the type of prey consumed and the behavior used to capture prey. Yet all occupy a similar position in the community, that of a high-level carnivore. Of the 19 species included in this study, all consumed actively moving prey frequently and, with the exception of *N. gibberifrons*, active prey dominated diets. Although the diets of the prey are poorly known, at least some, like *Bovallia gigantea*, *Harmothoe spinosa*, and *Sterechinus neumayeri*, are themselves high-level carnivores (Bone 1972; Brand 1976).

In this study the nototheniids show the greatest diversity in both diets and feeding behaviors although a high degree of similarity in diet

TABLE 7.—Seasonal dietary changes in fishes of similar size collected at the same locale off the Antarctic Peninsula. 1975. A χ^2 test for association was used to examine changes in the volume of each taxon consumed. A Wilcoxon sum of ranks test was used to examine changes in feeding intensity.

Species	Area	Date	n	$\overline{SL}$ (mm)	Range (mm)	No. taxa consumed	Volume		Fullness index		
							χ^2	P	$\bar{X}$	R	P
Notothenia gibberifrons	Peltier Chan.	Summer	30	146	106-217	13			6.8		
		Spring	49	138	100-229	13	31.3	<0.01	6.0	1,301	<0.30
	Brabant I.	Summer	25	134	87-260	12			7.5		
		Spring	22	123	106-167	9	114.6	<0.01	2.1	294	<0.01
Notothenia nudifrons	Low I.	Summer	20	107	72-140	8			5.6		
		Spring	34	95	47-127	5	80.9	<0.01	5.8	500	<0.74
Notothenia larseni	Low I.	Summer	27	114	84-152	8			6.6		
		Spring	25	99	90-142	9	66.7	<0.01	9.5	544	<0.08
	Brabant I.	Summer	29	120	70-150	4			8.1		
		Spring	30	86	60-126	5	27.9	<0.01	2.2	735	<0.04
Trematomus scotti	The Sound	Summer	8	112	88-134	5			6.4		
		Spring	7	101	85-114	5	109.4	<0.01	3.4	47	<0.20

TABLE 8.—Percentage diet similarity by number of prey items consumed (upper triangle) and point volume (lower triangle) in fishes taken off the Antarctic Peninsula, 1975.

	Notothenia neglecta	*Notothenia gibberifrons*	*Notothenia nudifrons*	*Notothenia larseni*	*Notothenia kempi*	*Trematomus scotti*	*Trematomus newnesi*	*Trematomus bernacchii*	*Pleuragramma antarcticum*	*Cryothenia peninsulae*	*Artedidraco skottsbergi*	*Harpagifer bispinis*	*Prionodraco evansii*	*Parachaenichthys charcoti*
N. neglecta	—	58	63	46	33	26	37	89	5	8	61	86	18	71
N. gibberifrons	39	—	61	52	34	51	39	56	13	14	57	55	24	51
N. nudifrons	36	42	—	58	58	44	46	64	10	3	87	66	27	54
N. larseni	28	40	31	—	52	49	67	43	38	29	41	44	37	60
N. kempi	34	40	61	39	—	48	41	32	20	6	56	35	37	29
T. scotti	19	42	30	70	38	—	45	32	27	23	36	27	20	32
T. newnesi	28	31	32	72	34	62	—	43	32	56	42	41	33	55
T. bernacchii	52	37	50	27	42	34	39	—	10	5	66	93	25	77
P. antarcticum	16	11	6	61	22	61	79	18	—	26	10	7	67	30
C. peninsulae	3	11	3	55	10	53	70	12	76	—	2	2	10	23
A. skottsbergi	28	31	67	25	53	25	30	41	5	2	—	70	27	61
H. bispinis	27	33	52	26	38	23	30	41	4	2	66	—	24	72
P. evensii	25	34	49	46	53	46	50	38	35	23	49	44	—	28
P. charcoti	39	16	9	25	17	21	23	12	20	16	9	8	23	—

among similar species is often present. Results from other studies, using fewer species, are similar (Permitin and Tarverdiyeva 1972, 1978; DeWitt and Hopkins 1977; Richardson 1975; Moreno and Osorio 1977; Moreno and Zamorano 1980). This high diversity is attributable to diet changes with size of fish, capture locality, and season.

The harpagiferids, bathydraconids, and channichthyids tend to be more specialized than the nototheniids in both their choice of prey and in the method used to obtain it. Results for *Harpagifer bispinis* can be compared to those of Meier (1971), Richardson (1975), and Wyanski and Targett (1981). In all cases, *H. bispinis* was shown to consume amphipods overwhelmingly. *Artedidraco skottsbergi* consumed polychaetes and amphipods; similar results were reported by Wyanski and Targett (1981). No comparable data are available for the bathydraconids or the channichthyids examined in this study. However, the diets of the five channichthyids examined by Permitin and Tarverdiyeva (1972, 1978) show them to be specialized feeders and, with the exception of *C. aceratus*, planktivorous; my remarks regarding the diets of *P. macropterus* and *Cryodraco antarcticus* corroborate these findings.

The high degree of dietary similarity that I observed among certain fishes and the similarity of diets reported by Permitin and Tarverdiyeva (1972, 1978), and Richardson (1975) do not necessarily imply interspecific competition over food, but do suggest a complex trophic structure not normally associated with communities of high latitudes (Cushing 1975). The benthic fishes studied use a wide variety of mechanisms to assure a constant food supply. For the generalists, these include switching prey types and feeding strategies; the specialists consume prey types which are themselves capable of maintaining stable populations either by switching food by becoming inactive (Dearborn 1967) or by possessing a reproductive biology which in-

cludes high fecundity and long mean generations (Cushing 1975). These stabilization mechanisms provide a constant source of food despite disbalanced primary production. With this constant and relatively abundant food source, competition, which requires a limiting resource (Larkin 1963), does not appear to be common among Antarctic fishes. The fact that high diet similarity is observed argues against competition over a limited food resource as a major factor structuring Antarctic fish associations (Zaret and Rand 1971; Tyler 1972). Where competition may be important, e.g., in the pelagic-benthopelagic fish association, the major prey item is krill, which is abundant. However, this abundance may be temporary and of recent origin. This would obscure the importance of competition in structuring Antarctic associations and points to the need for further study.

The position of fishes in the trophic structure of Antarctic communities is also not well understood. All are carnivorous and many are second or third level carnivores. Whether or not these fishes are themselves consumed in large numbers by the abundant birds and mammals of the Antarctic is poorly known. Some birds consume small species or juveniles of large species (Watson 1975) and several species of seals are reported to consume fish (Dearborn 1965; Stonehouse 1972). However, the species consumed and the relative importance of fish in the diets of these predators remain unknown. It does appear that such predators do not have much of an impact on the large benthic fish populations, since the fishes are extremely slow growing and long lived (Emerson 1970). Thus the impact of heavy and unaccustomed predation (fishing) on this system could be very disruptive. Before extensive exploitation begins, the life history of the organisms to be harvested should be understood.

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THE EARLY LIFE HISTORY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

KEVIN M. BAILEY[1]

ABSTRACT

The early life history of Pacific hake, *Merluccius productus*, is described from laboratory and field studies. At ambient temperatures (11°-13°C) egg hatching takes about 100-120 hours; complete absorption of the yolk takes about 150-200 hours. Respiration rates for first feeding larvae at 12°C are 4.8-6.8 µl/mg per hour. Growth rates for at least the first 20 days are slow compared with other larvae in the California Current. First-feeding hake larvae require a daily ingestion of about 0.13 calories.

In this study I present information on the early life history of Pacific hake, *Merluccius productus*, including rates of development, starvation, growth, and metabolism. I have also used samples from Ahlstrom (1959) and others to examine the vertical distribution of eggs and larvae by size class. My objectives in examining these life history processes are to 1) evaluate the hypothesis that the availability of food directly after complete yolk-sac absorption is the critical factor in survival of larval Pacific hake and 2) to determine the relative length of time Pacific hake are in egg and yolk-sac stages and are most vulnerable to invertebrate predators.

The early life history of Pacific hake represents an interesting contrast to other fishes that spawn off the coast of California, including the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*. Compared with these other species the early life history of Pacific hake has been little studied. It is known that hake larvae live below the mixed layer in colder water, and that first-feeding larvae have large mouths, so they can feed on a wide spectrum of food particles (Ciechomski and Weiss 1974; Sumida and Moser 1980). Both the anchovy and mackerel have been subject to intensive investigation as models of the causes of egg and larval mortality. Eggs and larvae of both anchovy and mackerel are found within the warm upper mixed layer (Ahlstrom 1959). Compared with hake larvae, anchovy and mackerel have relatively small mouths at first feeding; thus, the size of ingested food particles is restricted (Hunter 1980). At least for first-feeding anchovy larvae, it has been shown that the availability of food of the proper size and in adequate densities is important to survival (Lasker 1975). The results of the present study, in particular the determination of the food requirements of hake larvae may indicate important differences in the survival strategies of these three fishes.

METHODS

Development and Growth

All laboratory experiments in this study were conducted using eggs collected at Port Susan, Wash. This stock is reproductively isolated from the Pacific hake spawning off the California coast (Utter 1969), but I am assuming that temperature-specific rates of metabolism of larvae hatching from Port Susan eggs are similar to the rates for larvae hatching from eggs spawned in the California Current because 1) egg size is the same, 2) temperature-dependent hatching times are the same (see results this study), and 3) growth to age 2 is the same (Kimura and Millikan 1977).

Eggs were collected with a 500 µm mesh meter net (equipped with a cod end designed to capture live zooplankton) and returned to the laboratory at 5°-10°C. Eggs and larvae were reared in filtered seawater in 1-4 l jars containing 50 ppm each penicillin G potassium and streptomycin sulfate. Egg hatching experiments were done with 3 replicates of 10-20 eggs/l. Percent hatching was checked every 12 h. The eggs used in these experiments were without visible embryos

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and were assumed to be about 12 h old. The time to 50% hatching was determined by interpolation from the linear regression of percent hatching (y) against time (x). Confidence intervals on the 50% hatch time were calculated from the prediction of x from y as:

$$\text{C.L.} = \bar{x} + \frac{b_{yx}(y_i - \bar{y})}{D} \pm H,$$

where $D = b_{yx}^2 - t^2_{(0.05, n-2)} S_b^2$, and

$$H = \frac{t_{(0.05, n-2)}}{D} \sqrt{S_{yx}^2 \left[D\left(1 + \frac{1}{n}\right) + \frac{(y_i - \bar{y})^2}{x^2} \right]}$$

Time to 50% yolk-sac absorption was determined similarly. Survival of yolk-sac larvae appeared to increase substantially under lighting in the cold rooms, which raised temperatures in these experiments to 10.5°C in the 8°C room and to 13.7°C in the 12°C room. The 15°C room was consistently lighted. After hatching at temperature, postyolk-sac larvae were removed, placed in new jars, and observed to determine time to starvation.

Growth was examined by counting daily increments on otoliths. For verification of otolith increments as daily marks, larvae were reared in the laboratory without antibiotics in a 12-h light-dark cycle. Larvae were fed *Artemia salina* nauplii and natural zooplankton strained through a 216 μm mesh net at a concentration of about 1 animal/ml. Field-caught specimens were obtained from several cruises off the California coast in 1977, 1978, and 1979. Both laboratory-reared and field-caught specimens were preserved in 80% ethanol. Larvae were measured (standard length) and otoliths were removed under a dissecting microscope fitted with a polarizing filter. Otoliths were mounted on a glass slide in protex or euparal, and rings on the otoliths were counted at 600-1000× magnification.

Larval dry weights (preserved in 80% ethanol for otolith investigations and in 3% Formalin[2] for respiration investigations) were determined on a Cahn 25 Electrobalance after rinsing the larvae in distilled water and subsequently drying them for 24 h at 60°C. Weight loss due to preservation was determined by comparing weights of subsamples of fresh-frozen larvae and preserved larvae, all hatching from the same cohort of eggs. Shrinkage in length was determined by measuring anaesthetized larvae before preservation and then again after 2-3 wk of preservation in 80% ethanol or 3% Formalin. Shrinkage due to preservation delay and death in a wet cod end during or after a plankton tow was simulated by anaesthetizing and measuring larvae, and then placing them on seawater-wetted paper towels for specific time periods. Larvae were then preserved in Formalin. These preservation effects were tested only on first-feeding larvae.

Growth, egg development, and yolk-sac absorption data were fitted with a Gompertz curve using a least-squares nonlinear curve fitting program (SPSS). The Gompertz growth function was selected because it is a flexible nonlinear function commonly used in studies of larval fish (Zweifel and Lasker 1976).

Metabolic Rates

Respiration rates of larvae were measured using a micro-Winkler technique (Carritt and Carpenter 1966). Experiments were conducted in 30 ml glass stoppered jars, at densities of 2-3 larvae/jar, in dim light for 11-14 h. Larvae in filtered seawater were acclimated to temperatures for 12 h. After the experiments were completed and oxygen fixed, jars were kept for 2-10 d at 8°C in the dark before titrating. Experiments were designed to include 3-5 replicates per temperature; however, when bubbles formed during the experiment (a constant problem at 15°) samples were discarded.

Vertical Distribution

Samples from vertical series of tows taken in 1954 and 1955 were reported by Ahlstrom (1959). I sorted and measured these samples to examine size-related vertical distribution. Pacific hake larvae from an additional three vertical series taken in 1969 were sorted and measured. Since there were no apparent day-night differences, all hauls, day and night, were combined. Nonstandardized data consisting of raw numbers per haul, uncorrected for volume of water filtered, were used since more detailed information did not exist for many hauls. Data on numbers of larvae caught per haul were classified into the depth interval where most of the tow took place.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Development Times

Egg hatching time shows a marked response to temperature (Fig. 1). Time for 50% hatching of eggs collected at Port Susan ranges from 3.5 d at 15°C to 4.5 d at 12°C (coastal temperature range at 50 m depth is 11°-14°C) and 6.5 d at 8°C (the approximate temperature at Port Susan). Also shown in Figure 1 are the mean hatching times of eggs collected off California that were reported by Zweifel and Lasker (1976).

The time from hatching to complete absorption of the yolk sac is also temperature dependent (Fig. 2). The time for 50% of the sample larvae to completely utilize their yolks is 9.7 d at 10°C, 6.4 d at 12°C, and 4.2 d at 15°C. I was not able to rear larvae to yolk-sac absorption at 8°C. At 8°C, 8-12 d old larvae still had considerable yolk supplies and no functional mouth. A well-developed mouth normally formed after 4 d at 12°C and after 3 d at 15°C.

Both the mean and the maximum length of time to starvation after complete utilization of the yolk decreased with increasing temperature (Table 1). A nonparametric analysis of variance (Kruskal-Wallis; Conover 1971) indicates that temperature has a significant effect on the time to starvation ($P<0.01$). The variance in the mean time to death was large in these experiments due to death occurring not only from starvation, but from other causes such as being trapped in the surface film. These early nonstarvation deaths were excluded from the analysis.

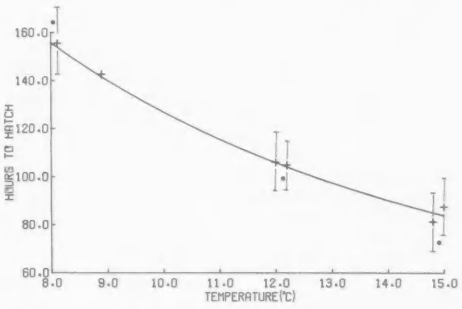

FIGURE 1.—Effect of temperature on time to 50% eggs hatching for Pacific hake, and 95% confidence intervals. Small solid circles are hatching times from Zweifel and Lasker (1976). Data was fitted to a Gompertz curve: $Y = 484.00 * \exp(-2.89 * (1 - \exp(-0.0623 * X)))$.

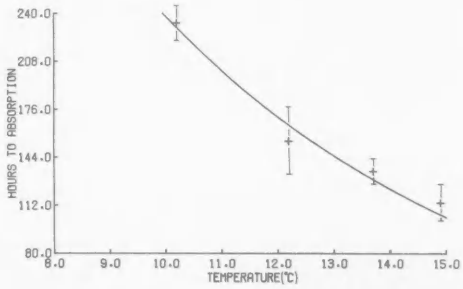

FIGURE 2.—Effects of temperature on 50% time to complete yolk-sac absorption for Pacific hake larvae and 95% confidence intervals. Data was fitted to a Gompertz curve: $Y = 1,269.52 * \exp(-108.82 * (1 - \exp(-0.0016 * X)))$.

TABLE 1.—Starvation experiments.

Temperature (°C)	Mean time to starvation (h)	Standard deviation	100% starvation (h)	No. of larvae
8	251.0	65.6	318	3
12	200.2	29.1	235	4
15	150.0	17.8	168	5

Growth Rates

Larvae were reared in the laboratory beyond the yolk-sac stage (±1 d) to verify otolith increments as daily marks. Increments begin to be added 1-2 d before complete yolk-sac absorption, perhaps coinciding with the onset of feeding; after yolk absorption, 1 ring is apparently added each day (Fig. 3). Rings on these otoliths were much fainter than those of field-caught specimens, possibly due to poor feeding, lighting, or other rearing conditions in the lab. Postyolk-sac larvae grown in the laboratory survived up to 10

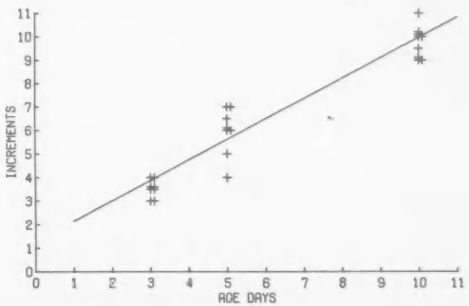

FIGURE 3.—The daily addition of increments by laboratory-reared postyolk-sac Pacific hake larvae.

d beyond the expected starvation date, but I was not able to maintain larvae much older than this.

The growth of field-caught larvae collected off California and stored in 80% ethanol was determined by otolith aging. Readings to 30 increments appear to clearly represent daily deposition of increments. However, after roughly 30 increments, dark bands appearing on the otoliths were separated by several inner rings and it was difficult to distinguish which were daily increments. R. Methot (Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif.) who read many of these otoliths from large larvae, felt that the larger bands were the daily marks. For the large otoliths I read, I followed this assumption.

The growth of Pacific hake larvae in length (not corrected for preservation effects) was fitted with a Gompertz curve (Fig. 4); however, a straight line provides a better fit for larvae <20 d old (Fig. 4, insert). Pacific hake larvae grow slowly in length for at least the first 30 d of posthatching life and then grow rapidly.

Growth in weight was examined by determining a length-weight relationship for larvae (Fig. 5a) and then combining this information with the age-length relationship described above (Fig. 5b). The weights used were from larvae preserved in 80% ethanol and uncorrected for pres-

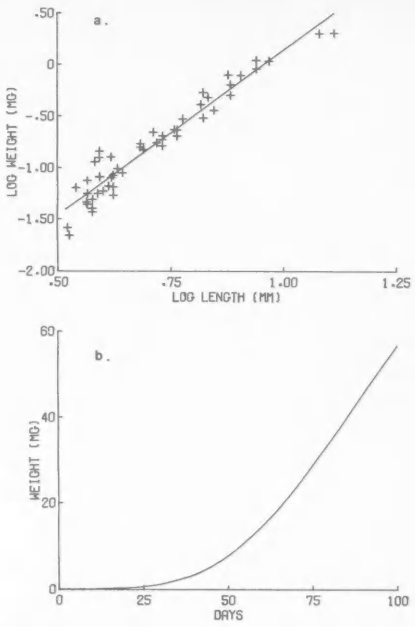

FIGURE 5.—Growth in weight of Pacific hake larvae. a. length-weight relationship of larvae off California (dry weights are from larvae preserved in ethanol), b. age-weight relationship.

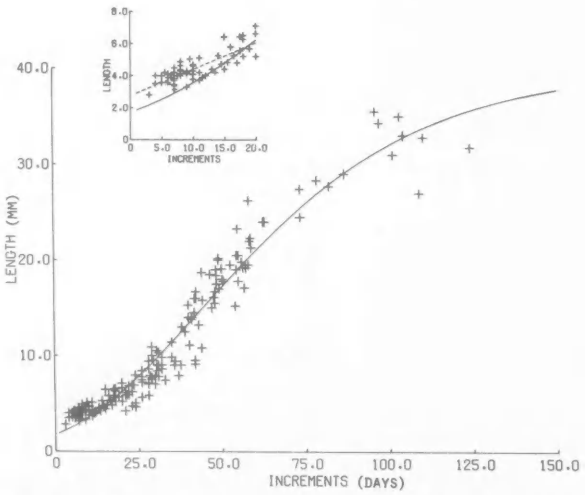

FIGURE 4.—The growth of larvae caught off southern California determined from otolith increments. A Gompertz curve was fit to the data, $Y = 1.72 * \exp(3.15 * (1 - \exp(-0.02624 * X)))$. Insert: daily growth for the first 20 d was fit better with a straight line: $Y = 2.75 + 0.16X$.

ervation effects. Increase in weight also appears to be slow for at least the first 30 d of posthatching life.

Weight loss of first-feeding larvae due to preservation in 80% ethanol was 57.8%, probably due mostly to loss of lipids and soluble proteins; weight loss in 3% Formalin was 24.1% (Table 2).

Shrinkage in length of first-feeding larvae preserved in Formalin was 8.9%; shrinkage of larvae preserved in ethanol was 3.6% (Table 3). Shrinkage due to delay in preservation was examined. Larvae in the 9-min delayed group decreased 17% in length, while those in the 29-min group decreased 40% in length. Most larvae, and especially larger larvae, probably do not die during the tow, and I have observed that in Puget Sound most larvae are alive after capture with a jar-type cod end. However, after a typical CalCOFI tow it probably takes an average of 5-10 min to remove and wash the cod end before preserving the larvae. I estimate that in routine sampling surveys small Pacific hake larvae probably shrink 9-20% in length due to handling. Shrinkage of large larvae was not tested and is probably different.

TABLE 2.—Weight loss due to preservation, determined by comparing fresh-frozen larvae to preserved larvae. Dry weights in milligrams.

	Live	80% ethanol	3% Formalin
Mean dry-weight (mg)	0.083	0.035	0.063
Standard deviation	0.007	0.004	0.006
No. of larvae	5	5	5
% of live weight	100.0	42.2	75.9

TABLE 3.—Shrinkage in standard length of first-feeding larvae due to preservative and related to delay in time of preservation, determined by comparing standard lengths of live larvae with preserved larvae. Three larvae per treatment; lengths are in millimeters.

	Ethanol	Formalin			
Preservative:	80%	3%	3%	3%	3%
Minutes delay	0	0	9	16	29
Mean live length	4.44	4.63	4.52	4.46	4.52
Mean fixed length	4.28	4.22	3.73	3.70	2.71
% length loss	3.6	8.9	17.5	17.0	40.1

Metabolic Rates

Respiration rates for Pacific hake larvae increase as a function of temperature and size (Fig. 6; Table 4). The experimental temperatures represent the range encountered by hake larvae within the spawning region. At 12°C, the mean temperature larvae experience off California,

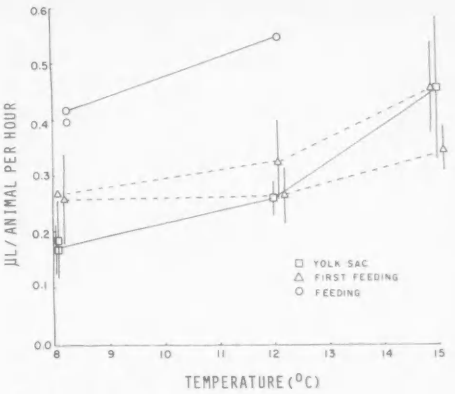

FIGURE 6.—The effect of temperature on mean respiration rates (µl/animal per h) of Pacific hake larvae of different stages. Vertical bars are ±1 standard deviation.

respiration rates for first-feeding larvae are 4.8-6.8 µl/mg-dry wt per h. These respiration rates were determined in 30 ml bottles, which did appear to slightly impair the swimming activity of larvae. Consequently, these rates are considered to be within the range between routine and active metabolism. The dry weights reported in Table 4 are of Formalin-preserved larvae, uncorrected for weight loss due to preservation. With the correction, weight specific rates would be 25% lower.

Vertical Distribution

Ahlstrom (1959) noted that Pacific hake eggs (and also most unsized hake larvae) were aggregated near the base of the mixed layer. From my analysis, most small larvae <8 mm were caught in the 50-100 m depth interval (Fig. 7), which corresponds to Ahlstrom's observations. Larger larvae were caught deeper; however, large larvae near the surface may be more able to avoid capture. An analysis by Lenarz (1973) indicates that larger larvae are probably able to avoid plankton nets in daytime. Large larvae, >12 mm, appear to be close to the surface later in the year (May-June), and have been caught at depths of only 25-50 m in nighttime plankton tows (A. Alvariño[3]). From my own observation in June

[3] A. Alvariño, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1979.

TABLE 4.—Summary of respiration experiments. Dry weights are of Formalin preserved larvae, uncorrected for weight loss due to preservation.

Temperature (°C)	Experiment	Mean length (mm)	Mean weight (mg)	Replicates	Larvae/jar	µl/animal per h	SD	µl/mg-dry wt per h
8	a. yolk sac	—	—	3	3	0.170	0.044	4.47
	b. yolk sac	3.49	0.038	3	5	0.185	0.072	4.87
	c. 1st feeding	3.81	0.049	2	2	0.271	—	5.53
	d. 1st feeding	3.97	0.055	4	3	0.260	0.083	4.73
	e. feeding	3.95	0.068	3	1	0.402	0.244	5.91
	f. feeding	3.97	0.070	2	1	0.426	—	6.09
12	a. yolk sac	—	—	—	—	—	—	—
	b. yolk sac	3.49	0.038	4	3	0.261	0.027	6.87
	c. 1st feeding	3.81	0.049	3	2	0.332	0.066	6.78
	d. 1st feeding	3.97	0.055	3	3	0.265	0.052	4.82
	e. feeding	—	—	—	—	—	—	—
	f. feeding	3.97	0.070	2	2	0.549	—	7.84
15	a. yolk sac	—	—	—	—	—	—	—
	b. yolk sac	3.49	0.038	4	3	0.460	0.126	12.11
	c. 1st feeding	3.81	0.049	3	3	0.467	0.080	9.53
	d. 1st feeding	3.97	0.055	4	3	0.345	0.041	6.27
	e. feeding	—	—	—	—	—	—	—
	f. feeding	—	—	—	—	—	—	—

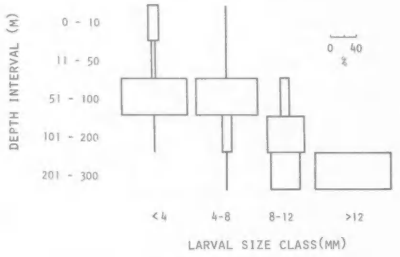

FIGURE 7.—The vertical distribution of Pacific hake larvae off the California coast shown as the percent of larvae within each depth interval by size class. Sample numbers are 1174, LT 4 mm; 1051, 4-8 mm; 19, 8-12 mm; 5, GT 12 mm; total sample of 2,249 larvae.

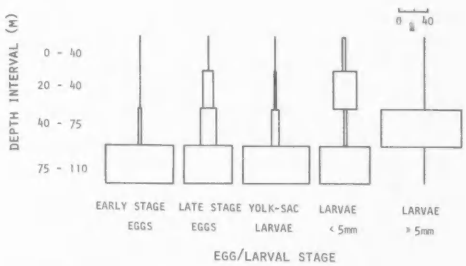

FIGURE 8.—The vertical distribution of Pacific hake eggs and larvae at Port Susan, Wash., shown as the percent of eggs or larvae within each depth interval by developmental stage or size class. Sample numbers: early stage eggs, 2,845; late stage eggs, 1,147; yolk-sac larvae, 409; larvae LT 5 mm, 31; larvae GT 5 mm, 12; total sample of 4,444.

1979, large larvae were also caught in midwater trawls near the surface in nighttime.

In contrast to eggs and larvae off the California coast, which are found at midwater, Pacific hake eggs and larvae in Puget Sound are located near the bottom of the water column. This is shown in Figure 8 for animals sampled at Port Susan (maximum depth, 110 m). This trend was also observed for animals collected at Dabob Bay (maximum depth, 175 m); the majority of eggs and larvae were found in the bottom 25 m of the water column. The difference in vertical distribution between eggs off California and eggs in Puget Sound may be explained as follows. The water at a reference level of 100 m is less saline (29.3‰) and less dense (1.0228) in Puget Sound than water off the California coast (33.6‰ 1.0258). Off California, eggs are spawned at 200-500 m depth, are relatively buoyant compared with the surrounding water, and rise upward to a level of equal buoyancy. Eggs in Puget Sound are spawned near bottom (Thorne 1977). Assuming that they are about the same density as the California eggs, these eggs are relatively less buoyant in the less dense water of Puget Sound, and therefore remain near the bottom.

DISCUSSION

Compared with eggs and larvae of other fishes in the California Current system, rates of development, growth, and metabolism of Pacific hake eggs and larvae are slow. These factors may be indicative of survival tactics (Hunter 1980), and differences could reflect the relative importance of certain environmental conditions, such as food abundance and predation pressure, in larval sur-

vival. Hunter (1980) contrasted several types of life history tactics for larvae of marine fishes. He indicated that in relatively cold water, where metabolic costs are low, a tactic of slow growth, feeding on large prey, and passive hunting may be common. This does appear to be the strategy of Pacific hake larvae. This tactic is quite different from that of high metabolism, fast growth, and active hunting demonstrated by other larvae, such as Pacific mackerel and to a lesser extent northern anchovy. Larvae of Pacific hake are located in colder water than larvae of Pacific mackerel and northern anchovy (Ahlstrom 1959) and compared with these other species the growth of Pacific hake larvae is slow (Fig. 9). Metabolic rates are difficult to compare because of different experimental techniques, but as a lower limit (due to the restrictive container size), 3-5 d old Pacific mackerel larvae require about 0.411 μl-O_2/animal per h at 19°C (Hunter and Kimbrell 1980). This compares with 0.265 μl-O_2/animal per h for first-feeding Pacific hake larvae at 12°C from this study.

I have calculated the energetic requirements of a first-feeding Pacific hake larva based on the routine metabolic rate at 12°C (the ambient temperature off the California coast) and growth in weight for larvae caught in the field, after correcting for preservation effects (Table 5). These values were converted to calories assuming values of 1 μl-O_2 = 0.005 cal and 1 mg-dry weight of larval fish tissue = 5.003 cal (Laurence 1977). The average first-feeding hake larva thus requires 0.091 cal/d to maintain and grow. This value is likely to be an underestimate of the caloric requirement due to an undetermined amount of energy needed to attack, capture, and digest prey animals. Estimates of assimilation coefficients range from 0.8 (Healy 1972; Dagg 1976) to 0.5 (Vlymen 1977). Assuming an assimilation coefficient of 0.7, as suggested by Ware (1975) and Laurence (1977), Pacific hake larvae would need to ingest 0.130 cal/d to satisfy metabolic and growth costs. Although this seems to be a reasonable estimate, significant errors may arise from the factors used for length-weight conversion, preservation effects, and from the assumed assimilation coefficient. I would suggest a more thorough examination of these factors in future experiments.

TABLE 5.—Caloric requirement of first-feeding Pacific hake larvae from growth and metabolism.

		Length (mm)	Weight (mg)	Corrected weight (mg)[1]
Growth:	day 4	3.412	0.0440	0.0694
	day 5	3.577	0.0512	0.0808

Weight gain = 0.011 mg/d = 0.0550 calories[2]
Respiration = 7.20 μl/d = 0.0360 calories[3]
0.0910 calories

Daily ration = Metabolism + Growth + Nonassimilated + Egestion
Daily ration × 0.7 = Metabolism + Growth
Daily ration = 0.130 calories

[1]Corrected for preservation effects.
[2]5.003 cal/mg-dry wt tissue (Laurence 1977).
[3]0.005 cal/μl-O_2 (Laurence 1977).

Using Sumida and Moser's (1980) report on the stomach contents of 3-4 mm Pacific hake larvae (Table 6), I calculated an estimate of daily ration that can be compared with the above estimate. Several approximations are necessary in this calculation, including 1) a feeding period of 12 h, 2) a digestion time, which I assume to be 5 h—ranges for other species are 3-8 h for herring (Werner and Blaxter 1980) and 2-4 h for Pacific mackerel (Hunter and Kimbrell 1980), and 3) a value of 5.2519 cal/mg-dry wt for copepods (Laurence 1976). The daily ration can then be calculated as: Daily ration = Stomach content weight × Feeding period/Digestion time (Feigenbaum 1979; Laurence 1977). For small Pacific hake larvae the daily ration thus calculated is 0.129 cal, which compares very closely with the previous estimate.

Hunter and Kimbrell (1980) calculated that 3-5 d old Pacific mackerel larvae require 0.143 cal/d to maintain and grow, based on the weight

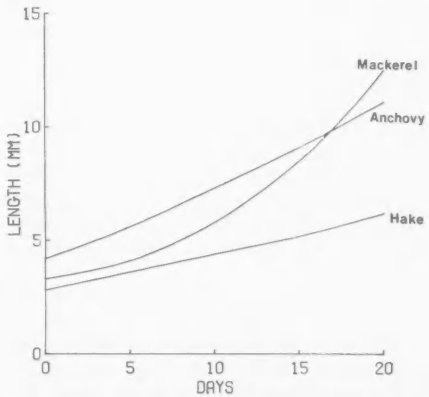

FIGURE 9.—Comparative growth of field-caught Pacific hake larvae (at 11°-14°C; this study), field-caught anchovy larvae (13°-16°C; Methot and Kramer 1979), and laboratory-reared Pacific mackerel larvae (19°-20°C; Hunter and Kimbrell 1980).

TABLE 6.—Average daily ration of 3-4 mm Pacific hake larvae (data from Sumida and Moser 1980, table 1). Number prey/stomach includes those with empty guts.

Prey organism	Total length (mm)[1]	Prosome length (mm)[2]	Dry weight (mg)[3]	No. prey/ stomach	Dry weight/ stomach (mg)
Adults					
Clausocalanus	1.15	0.70	0.006	0.38	0.00228
Paracalanus	1.0	0.57	0.004	0.29	0.00116
Calocalanus	1.0	0.57	0.004	0.08	0.00032
Oithona	0.95	0.52	0.003	0.03	0.00009
Calanoid unid.	1.04	0.60	0.004	0.09	0.00036
Disintegrated	1.04	0.60	0.004	0.08	0.00032
Copepodites					
Calanus sp.	1.50	1.00	0.050	0.02	0.00100
Oithona			0.002	0.03	0.00006
Calanoid			0.002	1.09	0.00218
Cyclopoid			0.002	0.03	0.00006
Disintegrated			0.002	0.21	0.00042
Nauplii			0.001	2.00	0.00200
Eggs			0.0005	1.06	0.00056
					0.01025

Calories per stomach = 0.01025 mg × 5.2519 cal/mg-dry wt[4] = 0.05383 cal.

$$\text{Daily ration} = \frac{\text{Calories in stomach} \times \text{Feeding period}}{\text{Digestion time}} \quad \text{(Feigenbaum 1979; Laurence 1977)}$$

$$= \frac{0.0538 \times 12}{5} = 0.129 \text{ cal/d.}$$

[1]From Brodskii 1967; Fulton 1968.
[2]From Total length = 1.16 × prosome length + 0.34; Fulton 1968.
[3]From Vidal 1978; Feigenbaum 1979.
[4]5.2519 cal/mg-dry weight conversion for copepods (Laurence 1976).

gain of laboratory-reared larvae and metabolic rates at 19°C. As they note this must be a lower limit. Assuming the same assimilation coefficient that I used for hake, 0.7, mackerel would need to ingest 0.204 cal/d to satisfy this ration requirement. First-feeding hake larvae have very large mouths compared with either mackerel or anchovy (Fig. 10), so they may feed on a wide size range of planktonic animals (including adult copepods); hake larvae could satisfy daily rations by capturing 25 nauplii or 15 small copepodites or 6 small calanoid adults or 1 *Calanus* adult. In contrast, both first-feeding mackerel and anchovy require a smaller size range of food particles (Hunter 1980). At least for anchovy, their survival depends on finding patches of small food organisms, such as the dinoflagellate, *Gymnodinium* (Lasker 1975). To satisfy its ration requirement a first-feeding Pacific mackerel larva would have to capture 4,000 *Gymnodinium* cells, 240 rotifers, or 39 copepod nauplii. It seems evident that they require high density patches of prey for successful feeding, whereas hake larvae may not require such dense patches of food for successful first-feeding.

From the results of this study, I infer that the first feeding of Pacific hake larvae is not as important to their survival as it is for Pacific mackerel and also for northern anchovy. This concept is supported by 1) the lower daily ration of hake larvae due to temperature-dependent activity and growth, 2) larger food items in the diet of hake larvae which provide more calories per prey item, 3) the relatively longer starvation time for hake larvae, i.e., they take 6-12 d to starve after complete yolk utilization, whereas anchovy take only about 4 d (Lasker et al. 1970), and 4) the ability of hake larvae to feed while still having yolk reserves (Sumida and Moser 1980). In addition, there is evidence of high energy wax esters in eggs of *Merluccius* (Mori and Saito 1966); thus larvae may have a longer safety period to find food. This concept does not exclude the possibility of a critical starvation period occurring later in larval or postlarval life, when stored energy reserves are exhausted and energetic demands are greater.

Predation may be relatively important as a factor influencing survival of Pacific hake larvae. Egg and yolk-sac stages of marine fish appear to be the stages most vulnerable to predation (Theilacker and Lasker 1974; Hunter 1980). Because of the colder temperatures that Pacific hake eggs and larvae inhabit, and resulting growth and development rates that are slow compared with Pacific mackerel (Hunter and

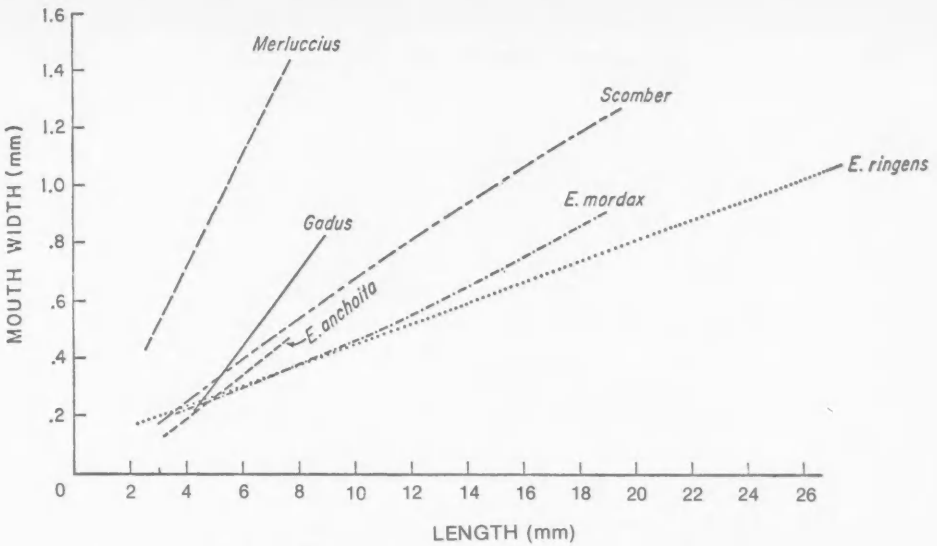

FIGURE 10.—Mouth sizes of larvae of hake, mackerel, anchovy, and cod by length class (Hunter 1980).

Kimbrell 1980) and northern anchovy (Zweifel and Lasker 1976), Pacific hake spend a longer time in vulnerable stages. Consequently, predation pressure on hake eggs and larvae may be high.

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THE BIOLOGY OF THE WHITE PERCH, *MORONE AMERICANA*, IN THE HUDSON RIVER ESTUARY

D. W. BATH AND J. M. O'CONNOR[1]

ABSTRACT

White perch, *Morone americana*, are found throughout a 250 km region in the Hudson River from Manhattan north to Albany, New York. They represent a dominant species in most portions of the river, although they are of little importance in the commercial fishery. Life history information was determined for more than 7,500 white perch collected from a 15 km region of the Hudson River between Haverstraw and Bear Mountain, New York.

Annulus formation began by the first week in May and was completed by the end of July. Maximum age for both male and female white perch was 7 years. Most of the growth occurred in the first 3 years for both males and females, and represented 78% of the length attained by the seventh year. Most fish were sexually mature by their second year. The length-weight relationship observed for Hudson River white perch was Log $W = -4.743 + 3.093$ Log L. The mean fecundity was 50,678 eggs per female, with a range of 15,726-161,449.

The white perch, *Morone americana* (Gmelin), inhabits rivers, bays, and estuaries of the Atlantic coast from Nova Scotia to South Carolina (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Leim and Scott 1966). The species has been introduced to freshwater lakes and reservoirs through migration, stocking, and by being landlocked in impoundments (Bigelow and Schroeder 1953; Mansueti 1961; Woolcott 1962). White perch has been reported in Lake Ontario (Sheri and Power 1969), Lake Erie (Larsen 1954; Trautman 1957), and the waters of Quebec (Scott and Christie 1963; Leim and Scott 1966). Most recently it has been introduced into the waters of Nebraska (Hergenrader and Bliss 1971).

White perch is found throughout a 250 km region in the Hudson River from Manhattan north to Albany, N.Y. It represents a dominant species in most portions of the river (McFadden[2]), although it is of little importance in the commercial catch (Sheppard[3]). The species is particularly abundant in the Hudson River from Nyack north to Catskill, N.Y. (Perlmutter 1967).

With the exception of a fecundity study (Holsapple and Foster 1975), no life history information for white perch in the Hudson River has been published. Site-specific data for white perch populations are available in reports (Raytheon Co.[4]; Lawler, Matusky and Skelly Engineers[5, 6]; Texas Instruments Inc.[7]). The present study was carried out to investigate the life history of white perch in the Hudson River estuary over a 15 km section, from Haverstraw to Bear Mountain, N.Y. This section of the Hudson River is a very stressful environment owing to frequent changes in salinity: On an annual basis, the region experiences one to several transitions between limnetic and oligohaline conditions (Abood 1974). The white perch is one of the highly adaptable species that can tolerate these changes. Along with the hogchoker, *Trinectes maculatus*, it is a dominant year-round resident of this portion of the Hudson region.

[1]New York University Medical Center, Department of Environmental Medicine, Laboratory for Environmental Studies, 550 First Avenue, New York, NY 10016.

[2]McFadden, J. T. 1978. Influence of the proposed Cornwall pumped storage project and steam electric generating plants on the Hudson River Estuary with emphasis on striped bass and other fish populations. Rep. for Consolidated Edison Co. of N.Y., Inc., 1179 p.

[3]D. J. Sheppard, New York State Department of Environmental Conservation, 50 Wolfe Road, Albany, NY 12223, pers. commun. March 1980.

[4]Raytheon Co. 1971. Indian Point ecological survey report II, January-June 1970. Submarine Signal Div., Portsmouth, R.I., 165 p.

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MATERIALS AND METHODS

We collected white perch at seven beach seining stations, nine trawling areas, and one experimental mesh gill net location between Haverstraw and Bear Mountain, N.Y., on the Hudson River from April through November 1970 (Fig. 1). Beach seine collections were made with a 30.4 m by 2.4 m seine (9.5 mm square mesh) or a 15.2 m by 1.5 m seine (6.5 mm square mesh), each with a central bag of 6.5 mm square mesh. The large seine was set from shore with the aid of a boat and retrieved in a semicircle. The 15.2 m seine was handhauled by pulling the seine parallel to the shore in water ~1.2 m deep. The large seine was fished in water ~2.4 m deep.

Bottom and surface trawls were made with a 7.6 m semiballon trawl, constructed with a 38.1 mm stretch mesh nylon body, with a 31.8 mm stretch mesh nylon cod end rigged with an inner liner of 6.5 mm stretch mesh nylon. Trawl doors were 1.1 m in length and 0.46 m in width. Tow

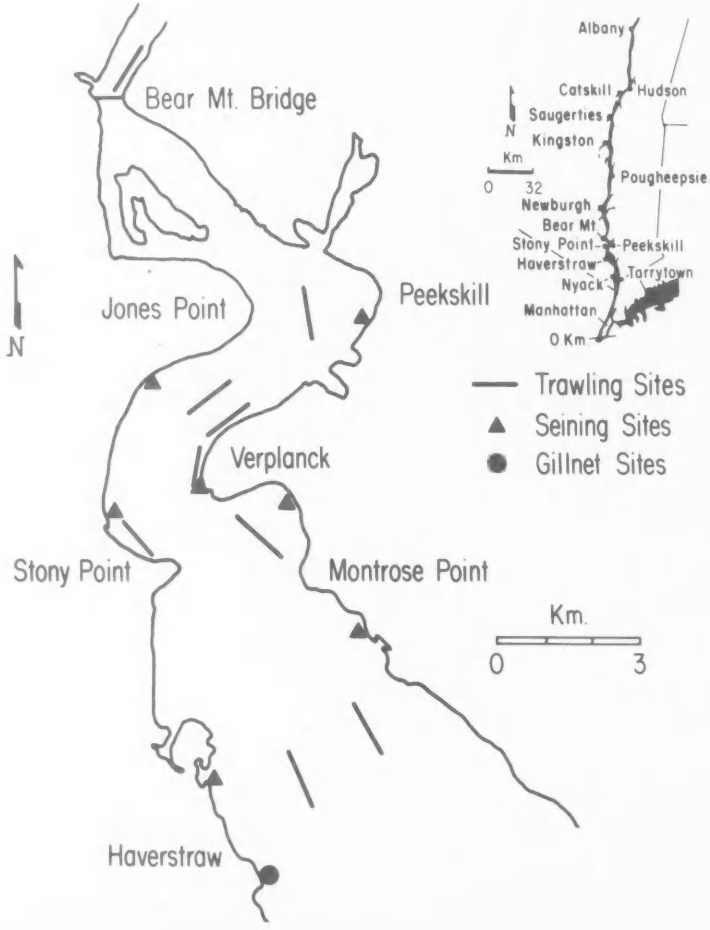

FIGURE 1.—Region of Hudson River from which white perch were collected.

speed for trawling was about 3.4 km/h. Details of the towing procedure are described in Bath et al. (1979).

The gill net was an experimental type with four panels of varying mesh size. The net measured 30.4 m by 1.8 m and contained 7.6 m each of 12.7, 25.4, 38.1, and 76.2 mm stretch mesh monofilament line. It was hung from 9.5 mm braided, polycore float line, with a bottom lead-coreline.

All fish collected at each site were immediately labeled and preserved in 10% Formalin[8] and returned to the laboratory for analysis. Each fish was measured (standard length (SL)) to the nearest millimeter, weighed to the nearest 0.1 g, and the sex was determined. A subsample of 310 fish was measured for fork length (FL) and total length (TL) to determine regression equations for comparison of Hudson River white perch populations with data from other river systems. Mature ovaries and testes were removed from selected individuals, weighed, and preserved in 10% Formalin. The ovaries were later transferred to Gilson's fluid for fecundity analysis (Ricker 1968). Stomachs were removed from randomly selected fish and preserved in 10% Formalin for later food analysis. Scales for age analysis were removed from behind the left pectoral fin (Rounsefell and Everhart 1953), cleaned, pressed, and sealed between glass microscope slides. The scales were read within 6 mo of the collection date.

[8]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Time of Annulus Formation

Annulus formation began by the first week in May and was completed in all age groups by the end of July (Table 1). Younger fish (age groups 1 and 2) completed the annulus by the end of June.

TABLE 1.—Percentage of aged white perch, *Morone americana*, with a new annulus and with a given number of circuli beyond the new annulus during a given period.

Date collected	Age (winters of life)	No. spec.	Percent with new annulus	Percent with noted no. of circuli beyond new annulus					
				0	1-2	3-4	5-6	7-8	>8
May 22-	1	11	73	64	9	0	0	0	0
June 2	2	36	50	50	0	0	0	0	0
(incl.)	3	36	39	39	0	0	0	0	0
	4	14	29	29	0	0	0	0	0
	5	14	0	0	0	0	0	0	0
	>5	31	0	0	0	0	0	0	0
June 9-	1	7	100	14	14	29	14	29	0
June 16	2	20	70	45	15	10	0	0	0
(incl.)	3	17	47	41	0	6	0	0	0
	4	14	43	22	14	7	0	0	0
	5	13	39	31	8	0	0	0	0
	>5	21	0	0	0	0	0	0	0
June 19-	1	5	100	0	0	0	40	20	40
June 30	2	7	100	29	14	57	0	0	0
(incl.)	3	8	50	50	0	0	0	0	0
	>3	9	33	33	0	0	0	0	0
July 1-	1	3	100	0	0	0	0	0	100
July 17	2	8	100	0	25	13	50	13	0
(incl.)	3	17	88	24	35	29	0	0	0
	4 or 5	6	83	67	16	0	0	0	0
	>5	5	20	0	0	0	0	0	0
July 24-	1	4	100	0	0	0	0	0	100
July 30	2	10	100	0	0	0	20	20	60
	3 or 4	7	100	43	57	0	0	0	0
	>4	2	100	100	0	0	0	0	0
Aug. 1-	1	10	100	0	0	0	0	0	100
Aug. 15	2	21	100	0	0	0	10	14	76
	3	9	100	0	11	33	33	11	11
	4 or 5	12	100	8	17	58	17	0	0
	>5	2	100	50	50	0	0	0	0
Aug. 17-	1	15	100	0	0	0	0	0	100
Aug. 31	2	4	100	0	0	0	25	0	75
	3	6	100	0	0	17	50	0	33
	>3	6	100	0	17	67	17	0	0
Sept.-	1	15	100	0	0	0	0	0	100
Oct.	2	5	100	0	0	0	0	0	100
	3	6	100	0	0	0	17	17	67
	>3	2	100	0	0	0	100	0	0

White perch of age groups 3 and older completed the annulus ~2 wk later.

Length-Frequency and Age Distribution

During May and June, there were three modes in the length-frequency data, with peaks at 65.0-69.0, 105.0-109.0, and 140.0-144.0 mm (Figs. 2, 3). These peaks represent the 1-, 2-, and 3-yr age groups. From July to November the length frequencies ranged from 10.0-14.0 mm to 200.0-204.0 mm (Fig. 4). The prominent mode at 50.0-54.0 mm represents young-of-the-year fish (Fig. 5).

Growth

The relationship between anterior scale radius and standard length for white perch from all age groups was $L = 32.64 + 45.56\,(R)$, where L = standard length in millimeters and R = scale radius in millimeters. The coefficient of determination (r^2) was 0.88 (Fig. 6).

The standard lengths at the various annuli were back-calculated and the growth histories were constructed for each year class, along with growth increments for each age group (Tables 2, 3). The most rapid growth occurred in the first 3 yr of life, and accounted for 78.0% of the total growth at the maximum size observed. Subsequent average growth increments were uniform among year classes, but considerably smaller (Fig. 7). Similar growth histories were compiled for each year class for both male and female white perch (Tables 4-7). Females grew slightly larger in TL than males of the same age (Fig. 8).

Length Conversions

We calculated the relationship between total length, fork length, and standard length measurements taken on a subsample of 310 white perch, ranging in size from 30.0 mm to 182.0 mm SL. A linear regression was computed to obtain conversions between the three methods so that we could compare growth rates among the different white perch studies. (Fig. 6). The relationship between total length and standard length was $SL = -1.05 + 0.81\ TL$, $r^2 = 1.0$; the relationship between fork length and standard length was $SL = -0.99 + 0.86\ FL$, $r^2 = 1.0$.

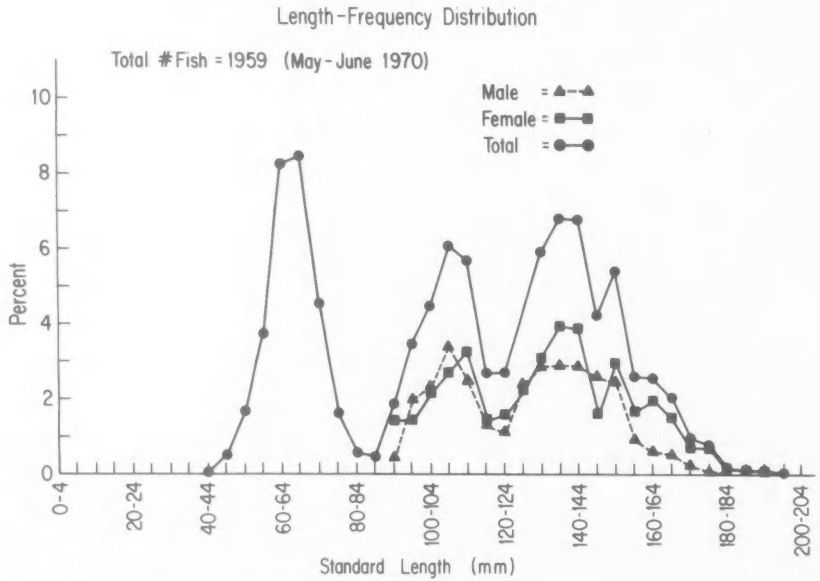

FIGURE 2.—Length-frequency distribution of white perch during May and June 1970, and for mature males and females during this same period.

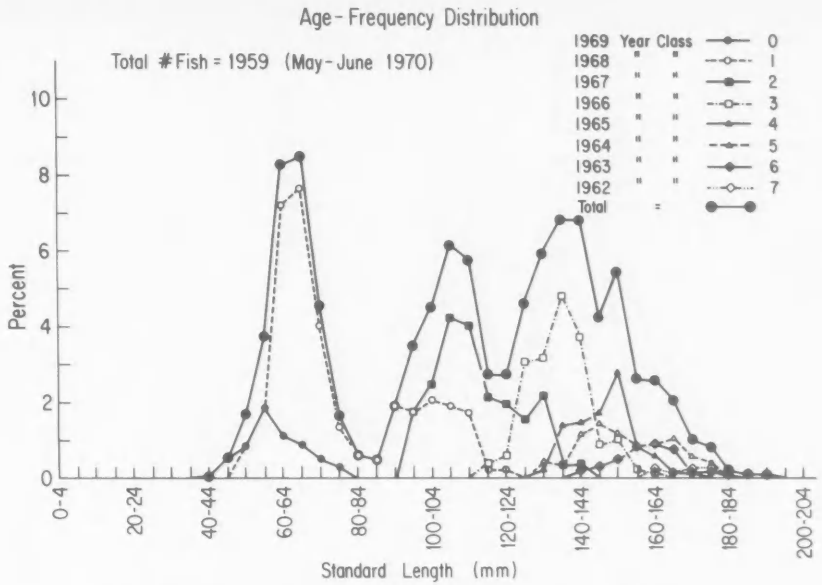

FIGURE 3.—Age-frequency distribution of white perch during May and June 1970.

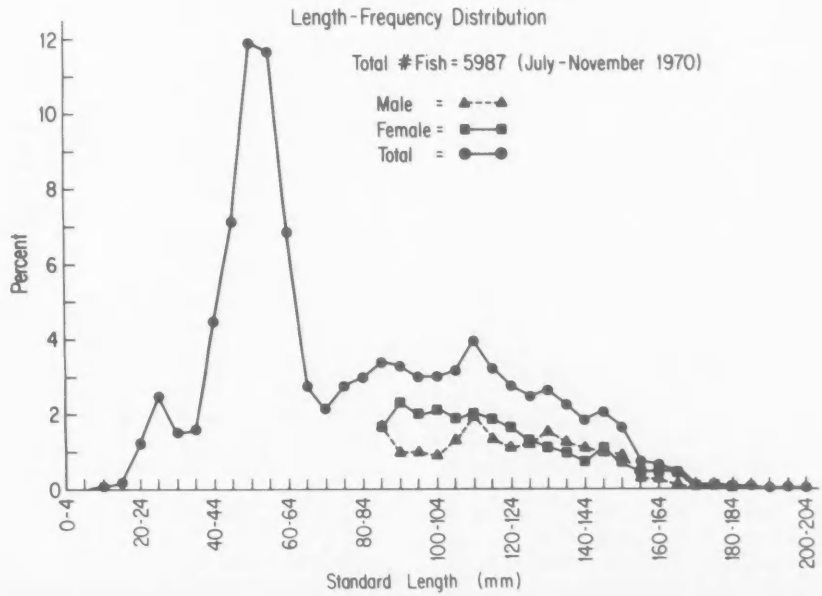

FIGURE 4.—Length-frequency distribution of white perch during July to November 1970, and for mature males and females during this same period.

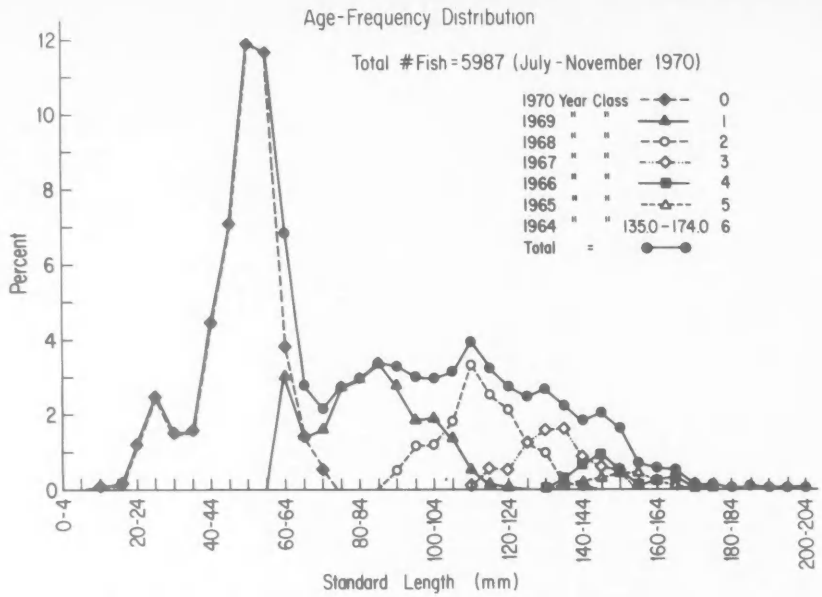

FIGURE 5.—Age-frequency distribution of white perch during July to November 1970.

TABLE 2.—Calculated growth of white perch in the Hudson River between Haverstraw and Bear Mountain, N.Y. (sexes combined), 1963-69.

Year class	No.	Calculated standard length (mm) at end of year						
		1	2	3	4	5	6	7
1963	12	69.2	119.2	150.1	164.2	176.2	185.9	194.1
1964	36	71.9	122.6	150.8	164.2	174.9	184.5	
1965	68	68.9	119.2	148.4	164.2	177.7		
1966	85	70.2	121.6	150.6	167.6			
1967	139	69.4	123.5	153.9				
1968	219	71.7	126.6					
1969	243	80.1						
Weighted mean		73.4	123.8	151.5	165.6	176.6	184.8	194.1
Increment		73.4	50.4	27.7	14.1	11.0	8.2	9.3
Percent of total growth		37.8	26.0	14.2	7.2	5.6	4.2	4.8
No.		802.0	559.0	340.0	201.0	116.0	48.0	12.0

Length-Weight Relationship

The length-weight relationship for Hudson River white perch was calculated using the least squares method (Ricker 1968). The relationship for males was Log $W = -2.262 + 1.925$ Log L, $r^2 = 0.706$. For females, the relationship was Log $W = -4.738 + 3.099$ Log L, $r^2 = 0.965$. The combined male and female length-weight relationship was Log $W = -4.743 + 3.093$ Log L, $r^2 = 0.952$. The values of the exponents 1.925 and 3.099 indicate females were heavier than males of the same length ($F_{1,20} = 4.97$; $\alpha = <0.05$). Graphically expressed (Fig. 9), it can be seen that this occurred for females over 140.0 mm (age group 2+ and older) and can be related to fatness and gonad development (Le Cren 1951).

Reproduction

Sixty-five female white perch collected during May and June (115.0 to 187.5 mm SL) and representing age groups 2 to 7 were analyzed for fecundity. An exponential curve was fitted to

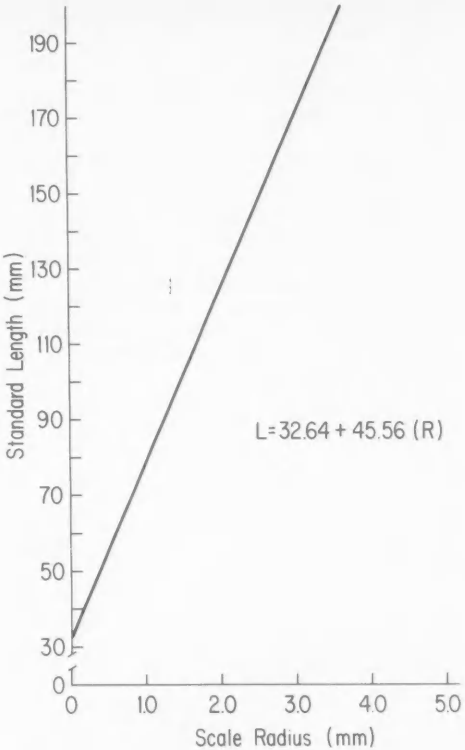

FIGURE 6.—Relationship between scale radius and standard length of white perch from the Hudson River between Nyack and Bear Mountain, N.Y. $r^2 = 0.88$.

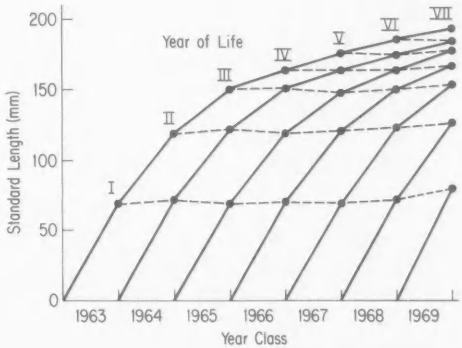

FIGURE 7.—Graphic representation of the growth histories of year classes of white perch from the Hudson River between Nyack and Bear Mountain, N.Y., 1963-69.

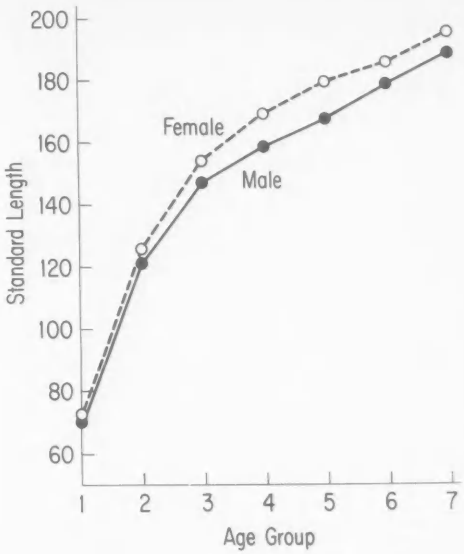

FIGURE 8.—Mean calculated standard lengths (mm) and increments of growth for each year of life of white perch from the Hudson River between Nyack and Bear Mountain, N.Y.

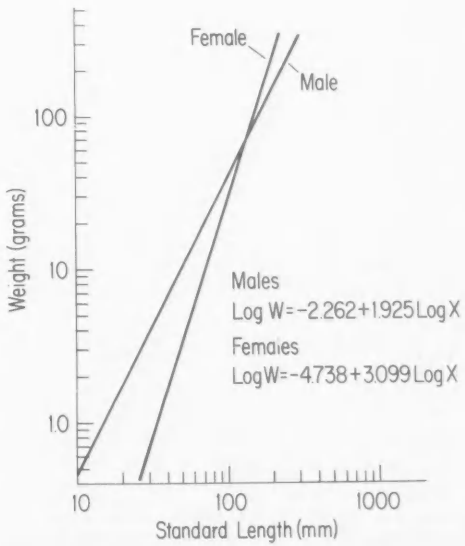

FIGURE 9.—Length-weight relationships of male and female white perch from the Hudson River between Nyack and Bear Mountain, N.Y. For males, $r^2 = 0.706$; for females, $r^2 = 0.965$.

fecundity data for May and June (Fig. 10). The egg-to-length relationship was $Y = 1{,}697.08e^{0.02X}$, where Y = number of eggs per fish and X = length, $r^2 = 0.39$. The white perch analyzed had a mean fecundity of 50,678 eggs/female with a range of 15,726-161,449.

The relationship between ovary weight and total body weight for 243 female white perch of known age collected from May to October is shown in Table 8. The changes in the ratio of ovary weight to body weight expressed as a percentage shows that spawning took place during June and was completed by July. Thereafter the ovaries are refractory and do not regain their weight until prior to the succeeding spawning season. The occurrence of the spawning season is further substantiated by the occurrence of white perch eggs and larvae in ichthyoplankton during June and July collections from the Hudson River (Lauer et al. 1974).

TABLE 3.—Growth history of the white perch in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Growth period	Growth increment for indicated year of life						
	1	2	3	4	5	6	7
1963	69.2						
1964	71.9	50.0					
1965	68.9	50.7	30.9				
1966	70.2	50.3	28.2	14.1			
1967	69.4	51.4	29.2	13.4	12.0		
1968	71.7	54.1	29.0	15.8	10.7	9.7	
1969	73.4	54.9	30.4	17.0	13.5	9.6	8.2

TABLE 4.—Calculated growth of white perch males in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Year class	No.	Calculated standard length (mm) at end of year						
		1	2	3	4	5	6	7
1963	2	66.9	115.2	142.3	156.8	169.3	179.7	189.1
1964	11	68.2	117.2	144.9	157.0	168.5	178.9	
1965	32	66.5	114.3	140.2	155.2	167.2		
1966	37	69.3	119.4	146.6	162.6			
1967	54	68.6	121.6	152.5				
1968	63	70.6	126.2					
1969	21	79.4						
Weighted means		70.0	121.2	147.2	158.8	167.6	179.0	189.1
Increment		70.0	51.2	26.0	11.6	8.8	11.4	10.1
Percent of total growth		37.0	27.1	13.8	6.1	4.6	6.0	5.3
No.		220.0	199.0	136.0	82.0	45.0	13.0	2.0

TABLE 5.—Growth history of the white perch males in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Growth period	Growth increment for indicated year of life						
	1	2	3	4	5	6	7
1963	66.9						
1964	68.2	48.3					
1965	66.5	49.0	27.1				
1966	69.3	47.8	27.7	14.5			
1967	68.6	50.1	25.9	12.1	12.5		
1968	70.6	53.0	27.2	15.0	11.5	10.4	
1969	70.0	55.6	30.9	16.0	12.0	10.4	9.4

Sex Ratio

Of the 2,600 mature fish collected, 1,209 were males and 1,442 were females, giving an overall sex ratio of 0.83 to 1.0 in favor of females. This phenomenon has been observed for other fish populations in which females attain an older age

TABLE 6.—Calculated growth of white perch females in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Year class	No.	Calculated standard length (mm) at end of year						
		1	2	3	4	5	6	7
1963	10	69.6	120.1	151.9	166.2	177.6	187.6	195.8
1964	25	73.2	124.4	151.4	165.8	175.6	185.6	
1965	29	70.4	121.9	152.8	170.1	183.8		
1966	41	70.6	123.2	154.6	171.7			
1967	67	70.5	125.6	156.2				
1968	98	73.0	128.6					
1969	35	78.8						
Weighted means		72.4	125.6	154.2	169.3	179.6	186.2	195.8
Increment		72.4	53.2	28.6	15.1	10.3	6.6	9.6
Percent of total growth		36.9	27.2	14.6	7.7	5.2	3.4	4.9
No.		305.0	270.0	172.0	105.0	64.0	35.0	10.0

TABLE 7.—Growth history of white perch females in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Growth period	Growth increment for year of life						
	1	2	3	4	5	6	7
1963	69.6						
1964	73.2	50.5					
1965	70.4	51.2	31.8				
1966	70.6	51.5	27.9	14.3			
1967	70.5	52.6	30.9	14.4	11.4		
1968	73.0	55.1	31.4	17.3	9.8	10.0	
1969	72.4	55.6	30.6	17.1	13.7	10.0	8.2

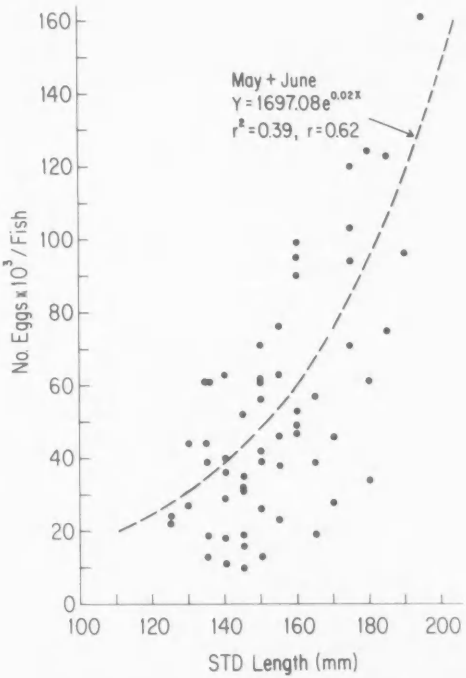

FIGURE 10.—Relationship between fecundity and standard length in female white perch collected during May and June from the Hudson River between Nyack and Bear Mountain, N.Y.

TABLE 8.—Mean ovary weight expressed as percentage of body weight.

Age	May	June	July	August	September	October
2	4.0	3.6	1.1	0.5	0.4	1.1
3	4.7	4.3	1.8	0.4	0.6	0.7
4	7.1	4.0	1.0	0.5	—	1.8
5	5.9	3.9	1.5	0.8	—	—
6	5.9	4.1	0.6	—	—	—
7	7.8	3.0	—	0.5	—	—

Total no. of fish 243

than males (Elrod and Hassler 1969). Chi-square analysis of data from individual collections showed the difference to be significant ($x^2 = 132.1$; $P < 0.001$). During May and June the population consisted of 70.1% mature males and females and 29.9% immature fish. From July to November the population consisted of 40.6% mature males and females and 59.4% immature fish. The change observed in the population between mature and immature individuals was due to the recruitment of young-of-the-year fish into the population sampled by our gear.

DISCUSSION

The growth and reproductive characteristics of white perch from the Hudson River compare favorably with data from other riverine systems. The maximum age attained in the Hudson River is about 7 yr, and maximum size is about 200 mm. Other data from the Hudson River (Lawler, Matusky and Skelly Engineers footnote 6; Texas Instruments Inc. footnote 7) show maximum age to be 7 and 9 yr, respectively, with a maximum size of from 200 to 222 mm. White perch from the Connecticut River, Conn. (Marcy 1976; Marcy and Richards 1974) attained a maximum age of about 8 yr, but grew to a maximum size of more than 280 mm. Wallace (1971) and Miller (1963) studied brackish water segments of the Delaware River estuary white perch populations and reported maximum ages of 8 and 10 yr, respectively. However, Wallace obtained a maximum size (~175 mm) smaller than found in Miller's (~257 mm) and smaller than in other riverine populations. White perch from the Patuxent River, Md., and the Roanoke River, N.C., had a greater maximum age, up to 10 yr; however, the size attained at 7 yr is approximately the same as in the Hudson River, from 190 mm to 205 mm (Conover 1958; Mansueti 1961). In Figure 11 we have plotted calculated standard lengths by age groups for white perch from five riverine systems. A similarity of growth rates for most populations is obvious except for the Connecticut River where perch grow more rapidly throughout their life span. Such rapid growth is more characteristic of white perch in freshwater impoundments than of riverine populations (Thoits 1958).

The rapid growth of perch in the Connecticut River may be attributed to a longer growing season; the onset of annulus formation occurs nearly 2 mo earlier than in the Hudson River. However,

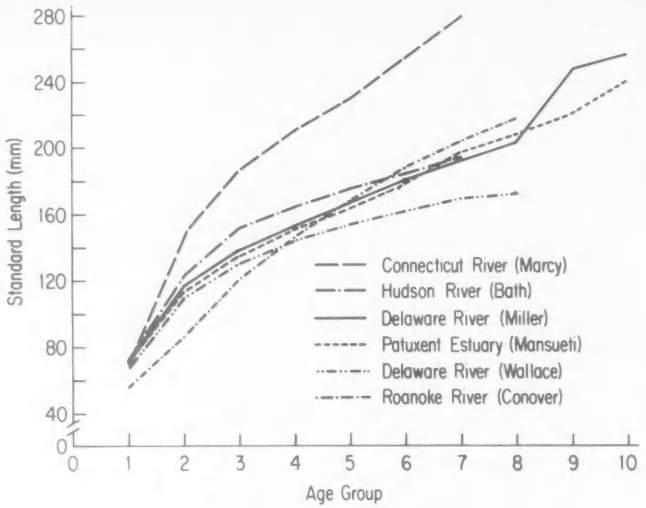

FIGURE 11.—Mean calculated standard lengths for white perch based on present and other studies.

this rapid growth rate estimate could be an artifact. Data from more recent year classes (1963-65) show lower rates of growth than observed from the 1959 through 1962 year classes (Marcy and Richards 1974). The Connecticut River population may be expanding rapidly and responding to increased population size with reduced rates of growth (Mansueti 1961).

White perch populations from south of the Hudson River show earlier onset and completion of the annulus. In the Chesapeake region, annulus formation begins in April (Mansueti 1961). In the estuarine portions of the Delaware River (Wallace 1971), the timing of annulus formation was shown to be complete by mid-June to early July. Lawler, Matusky and Skelly Engineers (footnote 5) reported that annulus formation in white perch from the Newburgh, N.Y., region of the Hudson River began in May and was completed by early July, essentially the same time observed in the present study. In Lake Ontario (Sheri and Power 1969) annulus formation was completed in July. The Connecticut River white perch (Marcy and Richards 1974) were anomalous in the apparent phenological trend of annulus formation, beginning in late March with completion during mid-May. This anomaly may be due to slightly higher average seasonal temperatures in the Connecticut River compared with those in the Hudson and Delaware Rivers, or it may be related to the fact that Marcy and Richards' (1974) studies were apparently carried out on a rapidly expanding population.

The basic reproductive potential for white perch, expressed as fecundity, appears to vary among the estuarine and freshwater populations studied. In estuarine and tidal rivers, fecundity values are similar throughout the range. White perch from the Roanoke River and Albemarle Sound, N.C., for example, had a mean fecundity of ~56,000 eggs/fish for age groups 3 and 4 (range 20,000-90,000; Conover 1958). Thoits (1958), in a generic study of white perch, estimated fecundity at 40,000 eggs/female. Hudson River fish fall close to this mean, with fecundity from three independent studies given as 21,000-135,000 (age groups 3 and 4; Holsapple and Foster 1975), 39,000-116,000 (Lawler, Matusky and Skelly Engineers footnote 6), and 16,000-161,000 with a mean of ~51,000 eggs/female in the present study. Variations in the data are most likely related to numbers of females sampled and the difficulty of obtaining fecundity data from a species which spawns over an extended period of time (Thoits 1958; Mansueti 1961; Taub 1969).

Freshwater lake populations of white perch may produce more eggs than similar groups in estuarine and tidal river systems. Au Clair (1956)

estimated the fecundity of white perch from Sebasticock Lake, Maine, at 164,000 eggs/female. Taub (1969), studying white perch from Quabbin Reservoir, Mass., gave a mean fecundity value of 271,000 eggs/female for age groups 3 and 4 (range 190,000-321,000). These fecundities, which are at least double that found in riverine populations, may be related to environmental factors such as food supply, sample size, time of capture, or technique used (Taub 1969). Growth data for these populations show that the increased fecundity is primarily related to an increased growth rate for white perch in lacustrine systems, and attainment of a greater size for mature females (Thoits 1958; Taub 1969).

The white perch does not contribute substantially to the commercial fishery of the Hudson River and has declined sharply from the 590 t (1.3 million lb) observed for the New York Bight region in the 1901 statistics (McHugh and Ginter 1978). Sheppard[9] reported that for the Hudson River the average catch between 1913 and 1964 was ~19,073 lb, ranging from 2,249 to 60,522 lb. The average commercial catch during 1965-74 was 1,600 lb.

However, the species has ecological importance in cycling nutrients within estuarine food webs and thus contributes to populations of commercially important marine and anadromous fisheries. The juvenile white perch in the Hudson River are prey for yearling and older striped bass, *Morone saxatilis*; adult white perch; and presumably other species such as the bluefish, *Pomatomus saltatrix* (Bigelow and Schroeder 1953; Texas Instruments Inc. footnote 7, 1976[10]).

The adaptability of the species to waters of different quality and chemical characteristics, and the high plasticity of fecundity and growth rate under various conditions (e.g., brackish waters vs. freshwater impoundments) suggest potential importance of white perch as highly suited to temperate zone aquaculture.

ACKNOWLEDGMENTS

Robert Koski kindly provided white perch for analysis. Scale analyses were verified by Dale Wallace, and Lois Peters assisted with statistical analyses. The assistance of Alfred Perlmutter was invaluable throughout the project in providing specimens and many helpful comments on the manuscript. We thank Gordon Cook for graphics, and Eleanor Clemm and Toni Moore for typing of the manuscript. The research was supported in part by the Consolidated Edison Co. of New York, Inc., and in part by the National Institute of Environmental Health Sciences, Grant ES00260 to the New York University Medical Center, Department of Environmental Medicine, Laboratory for Environmental Studies.

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IDENTIFYING CLIMATIC FACTORS INFLUENCING COMMERCIAL FISH AND SHELLFISH LANDINGS IN MARYLAND[1]

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ABSTRACT

In five of the seven most important commercial fisheries of Maryland an appreciable portion of the annual variations in catch can be linked with past fluctuations in the physical environment. The harvest figures were compared with appropriate annual characterizations of 40 years of daily environmental records using a variation of the stepwise multiple linear regression technique. The criterion for entry of a term into the regression was how well the given variable improved the prediction of a randomly chosen independent subset of catch figures. The identification of spurious predictor variables becomes less probable under this criterion. The results should help in the organization of further research and management concerning these species and may afford estimates of catches 1 or more years into the future.

Annual population levels of commercially harvested fish and shellfish usually fluctuate widely over the years. Such variation is often attributed to the influence of important environmental variables, such as water temperature, upon spawning success (Sissenwine 1978). Environmental variables may directly affect the mortality rates of prerecruits or indirectly exert influence by altering the abundance of forage or predators. Many other aspects of the ecosystem may also alter population levels (Cushing 1975); however, exact causative mechanisms in most fisheries are seldom known.

Year-to-year fluctuations in the abundance of exploited species will determine in part the magnitude of annual harvest of those species. But the relationship will not be completely deterministic, since landings will also be influenced by socioeconomic factors (e.g., prices and costs as they affect effort) as well as biological factors unrelated to exploitation (Ricker 1978). Despite these many complicating factors, significant correlations between various environmental variables and commercial landings of various species have been found in a number of fisheries. Dow (1977), for example, showed that temperature correlates well with the landings of 24 species of finfish, crustacea, and mollusks off the coast of Maine. Sutcliffe (1972) found freshwater input to St. Margaret's Bay to be a good indicator of fisheries production, possibly because of the stimulation of production caused by the nutrients in the runoff water. However, in neither case were the observed relationships demonstrated to help in predicting harvests, nor were the specific mechanisms responsible for the observed relationships rigorously delineated. In contrast, a regression model of brown shrimp landings off North Carolina, using temperature and salinity as independent variables, was found to be a reasonably accurate predictor of future landings (Hunt et al.[7]). Hunt's model has proven to be a useful management tool for this fishery, helping fishermen to decide how to gear up for the coming season.[8] Multiple linear regression has likewise been employed to explain variations in catch (e.g., Flowers and Saila 1972; Driver 1976). Only

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[8]M. W. Street, Chief, Fisheries Management Section, Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, P.O. Box 769, Morehead City, NC 28557, pers. commun. April 1981.

in the former instance, however, was there an attempt to validate the regression using independent data.

Thus, the value of correlative or regression models of fisheries is twofold: First, significant correlations can serve to guide research into identifying the causes of annual variation in catch; secondly, if validated, such models may forecast harvest in cases where more detailed deterministic models cannot be developed for lack of information.

The issue of model validation is especially important. Correlational models which best regress to the available data are often not the best predictors (Saila et al. 1980). In an effort to overcome this difficulty we have employed an amended version of stepwise regression analysis which does not rely solely on overall goodness-of-fit, but rather identifies those variables most likely to provide good predictions of data points not used in the actual regression.

To our knowledge multiple correlational models of the relationships between environmental variables and commercial landings in the Maryland portion of Chesapeake Bay have not been attempted in an algorithmic fashion. Because most of the dominant species reproduce in Maryland waters, the influence of environmental variation on harvest of these species may be particularly strong. Thus, we have developed multivariate regressions of the landings of major commercial species, using as predictors those environmental variables considered to have biological significance for the species being examined. Although measures of catch per unit effort (CPUE) would have been preferable as indicators of stock size, adequate effort data were not available. The results provide valuable insight into factors which may contribute to determining the population dynamics of these species and may also prove to be of value in establishing management practices.

SPECIES ADDRESSED AND DATA AVAILABLE

Seven dominant species in Maryland landings were selected for analysis. American oyster, *Crassostrea virginica*; blue crab, *Callinectes sapidus*; soft shell clam, *Mya arenaria*; and striped bass, *Morone saxatilis*, were chosen because they are the four species which yield the greatest dollar value to the Maryland economy. Menhaden, *Brevoortia tyrannus*, and alewife, *Alosa pseudoharengus* and *A. aestivalis* arbitrarily combined, were selected because they have been dominant in number of pounds harvested. The bluefish, *Pomatomus saltatrix*, was included because its harvest has increased dramatically in recent years, and there was interest in determining if this increase might be related to environmental variation.

A 33-yr record of annual catch data for 24 commercial species was available from records maintained by the Chesapeake Biological Laboratory and the NOAA Current Fisheries Statistics series. These records report the total Maryland landings (Chesapeake Bay and Atlantic Ocean) for each year. The Chesapeake Bay portion of the harvest heavily dominates the catches of the chosen species (85% or more of total). Because of the difficulty in obtaining sufficient information to separate Bay catch from the State total, the total was assumed to be representative of Chesapeake Bay.

ANNUAL CHARACTERIZATIONS OF ENVIRONMENTAL DATA

The environmental variables for which long-term records exist are water temperature, air temperature, salinity, and precipitation. All four have potential relevance to the levels of commercial harvest. Cross correlative relationships among these variables would be accounted for in the stepwise multivariate regression procedure employed in the analysis (discussed below). Daily recordings of these variables exist for a period exceeding 40 yr as taken from the Chesapeake Biological Laboratory pier at the mouth of the Patuxent estuary in Solomons, Md. Because this location is central to the Maryland portion of Chesapeake Bay, these data were assumed to be characteristics of conditions in the bay as a whole. Gaps in air temperature and precipitation from 1960 onwards were filled by data taken at the nearby Patuxent River Naval Air Test Center in Lexington Park, Md.

While catch figures represented the total landings for a season, environmental data existed with much finer temporal resolution. Our goal was to pair each annual catch figure with a value of an environmental property which might be representative of the effect that variable had on the stock during the year the daily readings were accumulated. One straightforward way of characterizing a year is to calculate the annual average of the variable in question. The stock,

however, may be more sensitive to shorter term deviations from this average. In an effort to quantify these deviations we devised four different ways of treating each of the original four time series to yield 26 annual series of environmental data.

The first of these methods, calculating the annual average, has already been mentioned. But the annual mean conveys little information on the cumulative amount of stress or benefit experienced by the populations because of the extreme high or low values of environmental variables. To portray the cumulative effects of these deviations, we defined variables analogous to the degree-days of agricultural science. Here the effect of a variable is assumed to be manifested only when its value goes beyond a certain "bias-level." If, for example, the organism is assumed to be cold stressed when the water temperature falls below 4°C, then 3 successive days of 1°C water temperature will contribute 9 degree-days towards the index of cold stress.

For each of the four variables recorded, a high and a low bias level were chosen so that when conditions exceeded these bounds at Solomons, we estimated that there were significant regions throughout the Maryland section of the Chesapeake Bay where fish and shellfish were probably stressed (or benefited) by the large excursions from the norm. These bias levels are shown in Table 1.

Of course, the fishery might be responding to individual episodes of stress, rather than the yearly cumulative value. We, therefore, elected to measure the lengths of the longest episodes during a year that a variable was beyond the bias values. These episodes were intermediate timescale phenomena (on the order of 1 to several weeks), and we wished to avoid contamination from high frequency events. For example, salinity may have remained above 16.2 ppt for all of a 28 d period, save on the 15th day when it dropped to 16.1 ppt. To characterize the episode as 14 d in duration would clearly be erroneous. To avoid such contamination we chose a "gap-interval" for each variable ranging from 3 to 5 d. If the variable went beyond the bias level for a duration not exceeding the gap interval, the episode was not terminated, although the days on which the lapse occurred were not tallied in the episode length. Thus, the episode of high salinities mentioned above would be counted as 27 d.

Finally, the possibility remains that the stocks might be acutely affected by short-term, intense stresses. We felt this eventuality would be reflected in the annual extremes of each variable.

These four operations, when applied to the four daily time series, yielded 26 annual time series of interest. (Cumulative and extreme low precipitations are uniformly zero by definition, and provide no information.) These series constituted the possible "predictor vectors" from which those yielding the best multiple regressions would be chosen. The values for the 26 variables calculated for the years 1938-76 are listed in Ulanowicz, Caplins, and Dunnington (1980).

TABLE 1.—Parameters used in calculating cumulative variables and episodes.

Variable	High bias	Low bias
Salinity	16.2 ‰	10.5 ‰
Water temperature	26.5°C	4°C
Air temperature	30°C	0°C
Precipitation	3 cm/d[1]	0 cm/d

[1]This value becomes 0.01 cm/d in calculating rain episodes, i.e., any day it rains is counted.

REGRESSION METHODOLOGY

In most fish stocks, year class size is considered to be established by the juvenile stage (Cushing 1975). For example, oyster spat set (analogous to juvenile stages of finfish) is a good indicator of spawning success (Galtsoff 1964). Thus, recruitment (and subsequently harvest) is often correlated to those conditions in the past which helped determine the level of juvenile success. In populations where all individuals in a year class are recruited into the fishery at the same age, and annual landings consist primarily of a single year class, a significant correlation might be obtained when the environmental variable in question was lagged against landings by the number of years equivalent to the age at recruitment.

For most species harvested in Maryland, recruitment is not simultaneous for all members of a year class; landings in 1 yr may consist of members of several or many year classes. Thus, environmental characteristics important to establishing year class strength may be partially correlated with landings recorded over several years, and vice versa. In order to account for such extended partial recruitment, stepwise regressions were employed, allowing the contribution of a given environmental variable to be assessed by successively lagging that independent variable by annual increments so as to encompass the lifespan of most of the stock being fished, i.e.,

harvests are regressed against conditions during the same year, 1 yr ago, 2 yr ago, etc.

In the case of species which do not spawn in Maryland and where environmental conditions in the Chesapeake Bay would not influence year class size (i.e., menhaden and bluefish), any significant correlations arising would either be the result of how the Chesapeake Bay environmental conditions influence the availability of the species to Maryland fishermen, or how its conditions might be correlated with critical conditions at the remote spawning site. Oysters and striped bass, being the longer lived of the species of interest, were regressed against conditions as long ago as 9 yr in the past. Conditions affecting the remaining species were investigated over the past 5 yr.

As mentioned in the introduction, we wished to limit our attention to those variables which are most likely to be good predictors of future harvests. In conventional stepwise regression, that variable which increases the goodness-of-fit by the greatest amount (usually measured by R^2, the percentage of the variance explained by the model) is included as the next variable in the regression equation. We chose instead to enter that variable which improved the model prediction of independent data points by the greatest amount.

To implement this alternate criterion we randomly chose 25% of our data to be reserved for testing. At each step in the regression all of the remaining variables were entered in turn into a least squares multiple regression using the remaining 75% of the data (employing subroutine GLH from the Univac[9] STAT-PAK library). The coefficients derived for each entry were then used to see how well they would predict the test values of the dependent variable. That variable whose inclusion generated the greatest improvement in fitting the test data (as measured by the sum of the squares of the deviations) was entered into the prediction equation.

Ivakhnenko et al. (1979) suggested that one should continue to include terms until the prediction can no longer be improved. It became apparent during the first few runs, however, that with six or eight degrees of freedom in the test data, statistically insignificant improvements in predicting the independent data were occurring. Accordingly, no variable was added to the prediction equation when its F-to-enter statistic (calculated on the fit to the test data) dropped below 3.5. This somewhat low level of confidence (a little below 90%) was chosen so as not to exclude potential predictors early in the screening process. It should also be pointed out that because of the small number of points in the test data, a relatively large percentage of the error in the test data must be explained to meet this F-to-enter criterion (40-60% in our trials).

By separating test and regression data in a random manner, it was always possible that by chance the set of test data chosen for any single run was unduly influenced by high or low production years. Such bias in the test data could result in a predictor accurate only under particular circumstances. Hence, it was necessary to run several (and in the later stages of the screening process, many) trials with different randomly chosen sets of test data. Presumably, the predominance of any single sequence of predictor vectors among the various trials would be an indication that the associated model might be a robust tool for forecasting. Once the functional form of the best predictor has been chosen, the parameters of this equation are redetermined using the full data set.

The sequence of searches outlined above should provide a necessary (although not sufficient) test for prediction formulae.

RESULTS AND DISCUSSION

To facilitate easy recognition of the environmental variables in the regression equations that are to follow, we adopt a two-letter, one-digit code to designate each of the 260 possible predictor vectors. The first letter will be either A, C, E, or X according to whether the processed variable represented an annual average, cumulative deviation, episode, or extremum, respectively. The second letter will designate air temperature, water temperature, daily precipitation, or salinity by T, W, P, or S, respectively. When it is necessary to distinguish between high or low deviations of these variables, the low values will be designated by writing the second letter in the lower case. Finally, the digit will designate the number of years lag behind the harvest figures. As examples, Cs3 would indicate cumulative low salinity 3 yr in the past, whereas EW2 would denote the longest episode of high water temperatures 2 yr ago.

After the field of predictor variables for each fishery had been narrowed to five or fewer, 1,000

[9]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Monte Carlo trials were run for each species using different random combinations of test data. In five of the seven species considered, pairs of two variables were identified frequently enough to warrant their being cited as potential predictor formulae in Table 2. In one case (blue crab) no variables appeared often enough in the trials to warrant reporting a predictor equation. By contrast several sequences of oyster predictors appeared often, but no sequence predominated in the trials. About five separate sequences appeared with almost equal frequency. Hence, no formula for oysters is cited.

In the clam regression, Cw1 appeared as the primary predictor in over 50% of the trials. In roughly 20% of these instances CS2 was included as secondary predictor. No predictor was chosen 12% of the time. When the two selected variables were finally regressed against the entire data set, 60% of the total variance was explained, 49% by Cw1 alone. Environmental data were available to assess the predictive value of this equation for the year 1977. As can be seen in Figure 1, this projected value has a large deviation from the recorded measure, but this deviation falls within the range of errors in the hindcast.

Interpretation of this equation in terms of causality is complicated by the absence of effort data. For example, the effects of the rise in number of licensed clammers (from 3 in 1952 to 100 in 1957 to 200 in 1979 [Richkus et al.[10]]) on catch cannot be accounted for, and they may have been substantial. Still, the strong correlation between cumulative low water temperature lagged 1 yr and catch suggests a causal relationship.

[10]Richkus, W. A., J. K. Summers, T. T. Polgar, and A. F. Holland. 1980. A review and evaluation of fisheries stock management models. Martin Marietta Laboratories, Baltimore, Md., 177 p.

In Maryland, soft shell clams spawn in spring and fall (Pfitzenmeyer 1962). However, the spring set each year is almost totally eradicated because of predation by benthic feeding fish and crabs which migrate onto Maryland clam grounds each spring and leave each fall (Holland et al.[11]). Factors influencing the strength of the fall set (which occurs from October through December) and the ensuing survival of juveniles have not been identified. It appears that these factors are the ones most likely to have the greatest effect on the magnitude of commercial clam landings. Since Maryland is near the southern

[11]Holland, A. F., N. K. Mountford, M. Hiegel, D. Cargo, and J. A. Mihursky. 1979. Results of benthic studies at Calvert Cliffs. Final Report to Maryland Power Plant Siting Program. Ref. No. PPSP-MP-28, 229 p. Martin Marietta Laboratories, Baltimore, Md.

TABLE 2.—Potential predictors of landings (in metric tons) of designated species; see text for code to predictor variables.

Species	Regression	Multiple R^2	F	df
Soft clam, *Mya arenaria*	$H_s = 372.4 + 13.56Cw1 + 3.765CS2$	0.60	11.1	22
Menhaden, *Brevoortia tyrannus*	$H_m = 888.4 + 45.99Ep5 - 9.126CT4$	0.53	11.1	30
Bluefish, *Pomatomus saltatrix*	$H_b = -48.20 + 1.948Ep5 + 0.1693Cs2$	0.60	14.8	29
Alewives, *Alosa aestivalis* and *A. pseudoharengus*	$H_a = 3,344 - 24.19Ep3 + 93.80Xt2$	0.51	10.5	30
Striped bass, *Morone saxatilis*	$H_r = 7,414 - 446.5AT3 + 2.435Ct1$	0.45	8.3	30

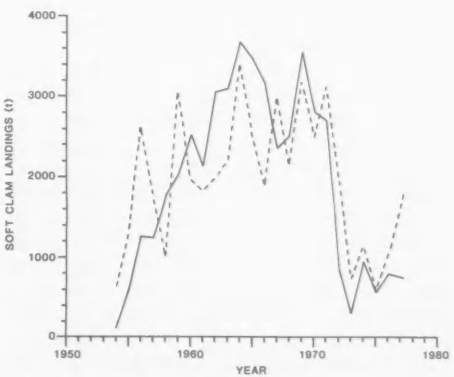

FIGURE 1.—Maryland soft clam landings in metric tons from 1952 to 1977 (solid line) and landings predicted using the regression model (dotted line) (Table 2). (Landings for 1977 did not enter into the derivation of the model.) Environmental factors were a cumulative low deviation in water temperature (with a 1-yr lag behind the harvest figure), and a cumulative high deviation in salinity (with a 2-yr time lag).

boundary of the geographical range of soft-shell clams (Manning[12]), cold water temperatures may, in some unexplained way, enhance the survival of a previous year's set.

Manning and Dunnington (1956) showed that Maryland clams grow at a rapid rate, achieving legal size (2 in, 5.1 cm) at an age of 16 to 22 mo. Hence clams spawned in the fall of one year would enter the commercial fishery during the spring 2 yr later. Extreme low water temperatures generally occur in January or February of each year and during some years coincide with periods of high salinities. Thus, both variables in the regression model could be exerting an effect on juvenile clams from set to the age of 6-7 mo, when they are approximately 0.5 cm (0.2 in) in size. Low water temperature may delay movement of predators into Maryland waters, permitting juvenile clams to grow to a less vulnerable size. High salinities during the juvenile life stages could also favor growth and rapid maturation of clams.

The remaining four regressions are composed of variables which are less readily explained. The two terms entering the menhaden regression have 4 and 5 yr lags (Table 2). But menhaden which make up Maryland landings are of ages 2 and 3, with almost no 4-yr-old fish taken (Merriner[13]). Thus, any causal mechanism suggested by the regression would have to be a second generation response, remembering that menhaden do not become sexually mature until ages 3 or 4. Ep5 appeared as the most important predictor in 37% of the trials with CT4 following as a secondary predictor in 23% of those cases. Menhaden catch is depicted in Figure 2.

Juvenile bluefish use Chesapeake Bay as a nursery area and there is the possibility that a distinct Chesapeake Bay stock of bluefish exists (Kendall and Walford 1979). Bluefish, being a marine species, are generally not found in low salinity waters, and their distributions can be well defined by salinity patterns (Lippson et al. 1980). Thus, the precipitation variable entering the regression (Table 2) may reflect diminished nursery habitat caused by high precipitation, resulting in a decline of harvestable fish in future

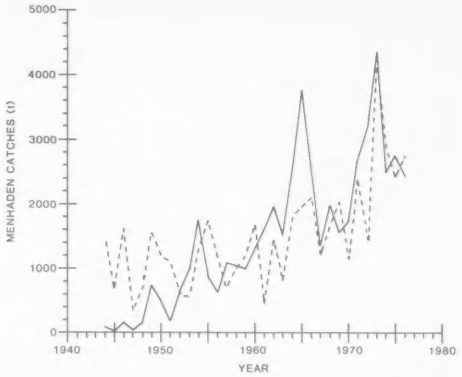

FIGURE 2.—Actual (solid line) and predicted (dotted line) catches in metric tons of menhaden, 1946-76, based on the regression model in Table 2. Environmental factors were an episode of low daily precipitation (with a 5-yr time lag behind the harvest figure), and cumulative high deviation in air temperature (4-yr time lag) which had a negative effect.

years. However, age composition of Maryland bluefish catch is unknown, and the particular lags in the regression are not readily explained. Bluefish harvests are illustrated in Figure 3. Ep5 appears as the primary predictor in 56% of the trials run with Cs2 following in 23% of those instances. It is noteworthy that the same variable (Ep5) appears as the most useful predictor of both menhaden and bluefish. Both species are coastal spawners, and it is entirely possible that

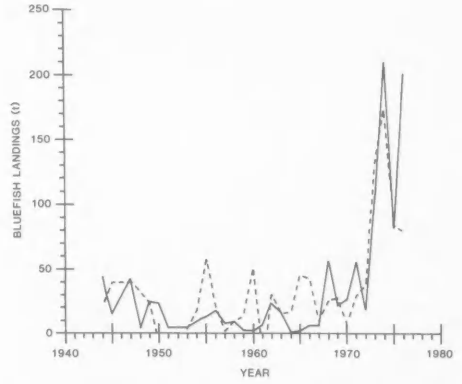

FIGURE 3.—Predicted (dotted line) and recorded (solid line) weights of bluefish landings in metric tons, 1947-76, based on the regression model in Table 2. An episode of low daily precipitation (5-yr time lag), and cumulative low deviation in salinity (2-yr time lag) were the environmental factors.

[12]Manning, J. H. 1957. The Maryland soft-shell clam industry. Study Report 2, 25 p. Maryland Department of Research and Education, Solomons, Md.

[13]J. V. Merriner, Chief, Division of Fisheries, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516, pers. commun. September 1980.

the same causal mechanism is affecting the catches of both fishes.

Both species included in landings as alewives, *A. pseudoharengus* and *A. aestivalis*, are anadromous, tributary spawners in Maryland (Hildebrand and Schroeder 1927). Thus, poor spawning success could readily be related to low freshwater runoff caused by low precipitation. However, the age of first spawning of these species is from 3 to 5 yr, with the majority spawning at 4 or 5 (Davis et al.[14]). The regression (graphed in Fig. 4) suggests the possibility that recruitment in Maryland occurs at a younger age, but data on the age distribution of the catch are unavailable to confirm or refute this suggestion. The other variable entering the alewife regression (Table 2) is lagged by 2 yr. Since fish taken in a given year would have been present in the Atlantic Ocean 2 yr before being harvested, this correlation is difficult to explain in a causal manner. Ep3 is the major predictor in 50% of the trials and is followed by Xt2 in 20% of those cases.

The least significant of all the predictors cited is the one for striped bass (see Fig. 5). Both terms show a favorable correlation with cold air temperatures over a season. Cold seasons are conducive to greater amounts of ice formation along river edges. The scouring from ice floes contributes high quality detritus to the riverine system to supplement the food source for zooplankton, in turn providing the larvae with abundant food (Heinle et al. 1976). Boynton et al.[15] have previously remarked that year class success correlates jointly with cold winters and high runoff. The chosen variables did not dominate the trials heavily. AT3 was the major predictor in only 33% of the trials, one-third of which were accompanied by the variable Ct1. Xs4 appeared as the major predictor almost as often (25% of the time there was no major predictor), but did not result in a significant correlation with the full data.

An examination of the power spectra of the errors of the five models (using subroutine POWDEN in Univac STAT-PAK) revealed no appreciable differences from the spectral pattern of random noise.

[14]Davis, J., J. V. Merriner, W. J. Hoagman, R. H. St. Pierre, and W. L. Wilson. 1971. Annual Progress Report, Anadromous Fish Project. Proj. No. Va. AFC7-1, 106 p. Virginia Institute of Marine Science, Gloucester Point, Va.

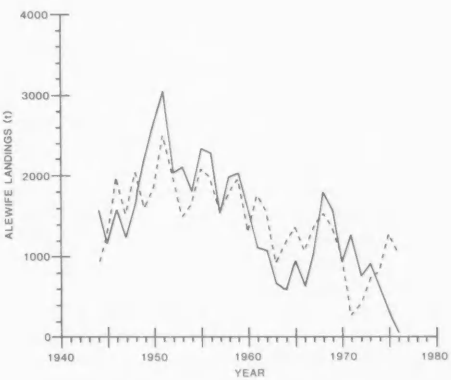

FIGURE 4.—Annual landings (solid line) in metric tons of alewife, 1944-76, as compared with predicted values (dotted line), based on the regression model in Table 2. Environmental factors were an episode of low daily precipitation (3-yr time lag) (negative effect) and an extremum of low air temperature (2-yr time lag).

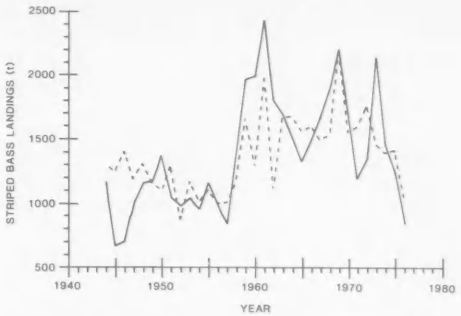

FIGURE 5.—Predicted (dotted line) and tabulated (solid line) landings in metric tons of striped bass from 1944 to 1976, based on the regression model in Table 2. Environmental factors were high annual average air temperature (3-yr time lag) (negative effect) and cumulative low air temperature (1-yr time lag).

CONCLUDING REMARKS

Perhaps the most significant observations to be made from this exercise involve the comparison of the results reported herein with those reported previously from a conventional search for

[15]Boynton, W. R., E. M. Setzler, K. V. Wood, H. H. Zion, M. Homer, and J. A. Mihursky. 1976. Potomac River fisheries program ichthyoplankton and juvenile investigations. Ref. No. 77-169CBL, 328 p. Center for Environmental and Estuarine Studies, Solomons, Md.

predictors using the same data (Ulanowicz, Ali, and Richkus 1980). The major predictors cited in the previous work were either identical to, or qualitatively similar to, the initial variables selected by the more usual analysis. In that earlier work up to seven terms appeared in one regression equation (F-to-enter criterion of 4.0), and R^2 values ranged as high as 0.86 with four variables. Despite having dropped the F-to-enter criterion below the 90% confidence level, the joint criterion that the variables chosen also be reasonably good "internal predictors" appears to have resulted in a more stringent combined test for selecting variables. Fewer spurious predictors are likely to appear using the new criteria. Although the regression with the full set of data will not be as tight as might otherwise be possible, there is less likelihood that predictions on independent data will be wildly in error. In the words of Ivakhnenko et al. (1979), the "fan of predictions" has been narrowed.

When the number of possible predictor vectors is large compared with the number of observations (as it is in this study), there is concern that multiple regression R^2 values can be inflated (Rencher and Pun 1980). Fortunately, the method described herein does not rely on R^2 values alone. Before a variable is chosen for further consideration, it must explain a significant fraction of the variance in several randomly assembled groups of test data. To see how well this might screen against including spurious variables, the search procedure for the menhaden predictor was rerun with the yearly observations randomly scrambled. Out of 28 possible trials with the original data, at least one variable was added in exactly half the trials (with an average F-to-enter of 9). In all but 2 of those 14 successes the first variable entered was identical (Ep). By contrast, only 5 successful trials were recorded with the scrambled data (average F-to-enter was 5), although one variable did appear in 3 of those successful trials. Nonetheless, there is an evident decrease in the frequency and number of variables with successful F-to-enter ratios in the trials with scrambled data. The only species studied giving results nearly as poor as the scrambled data was blue crab, and those findings were disregarded.

Unfortunately, the results of the present analysis must still be viewed with caution. Although the possibility of identifying a spurious correlation as a predictor has been decreased, it cannot be totally eliminated. The fact that substantial portions of the variability in landings of all the species considered can be explained by a few environmental variables suggests the important role which environmental conditions play in determining stock size. However, our inability to interpret many of these relatinships in a causal manner reflects both a lack of knowledge of mechanisms influencing fish population dynamics as well as an unfamiliarity with the auto and cross correlative relationships between the variables introduced into the regression process. (Because the procedure employed was stepwise, true causal variables may have been displaced in the regressions by spurious variables which by chance were closely correlated. No detailed analysis of the independent variable data sets was performed to address this issue. More analyses would be required to fully account for this possibility.)

Despite these limitations, the analyses appear to have been fruitful, particularly in the case of the soft clam. As for the other species, the value of the models will be determined when sufficient data are available to assess their predictive value for future landings. Only then can it be ascertained whether any chosen predictor was spurious or reflected some unknown causal relationship between environmental variation and stock dynamics. Meanwhile, the terms appearing in the regressions may engender new research projects into the mechanisms determining the sizes of these important fisheries stocks.

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AERIAL SURVEYS FOR MANATEES AND DOLPHINS IN WESTERN PENINSULAR FLORIDA

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ABSTRACT

Low altitude aerial surveys were conducted to count West Indian manatees, *Trichechus manatus*, and bottlenose dolphins, *Tursiops truncatus*, in western peninsular Florida. A total of 554 manatees was observed in 297 groups. Most of the manatees (58.5%) were sighted in the Collier-Monroe Counties in shallow, brackish inshore areas. A total of 1,383 bottlenose dolphins was observed in 431 herds, including 700 (in 146 herds) in the Gulf of Mexico, 491 (in 185 herds) in bays, and 192 (in 100 herds) in marsh-river habitats.

West Indian manatees, *Trichechus manatus*, and bottlenose dolphins, *Tursiops truncatus*, occur in rivers, estuaries, and coastal areas in Florida (Moore 1953; Layne 1965; Hartman 1974[3]; Irvine and Campbell 1978). Manatees are dispersed throughout Florida waters during the summer, but concentrate around warmwater sources in winter (Hartman footnote 3; Irvine and Campbell 1978). Aerial surveys indicate that bottlenose dolphins are also well dispersed in coastal waters of Florida (Odell 1976, 1979; Leatherwood 1979; Odell and Reynolds 1980[4]). However, localized distribution patterns and seasonal changes in distribution and abundance have only been documented in a few areas for manatees (Odell 1976, 1979; Irvine et al. 1978[5]; Shane 1980[6]) or dolphins (Odell 1976, 1979; Shane and Schmidly 1978[7]; Irvine et al. 1979[8]). The distribution of manatees and dolphins in various habitat types and salinities in Florida also is unclear.

More information is needed to serve as a basis for sound conservation and management decisions because manatees and dolphins are protected by the Marine Mammal Protection Act of 1972; manatees are also protected by the Endangered Species Act of 1973. Southwestern Florida, encompassing Everglades National Park (ENP; Monroe County) and the Ten Thousand Islands (Collier-Monroe Counties), is of particular interest because this area has been relatively unaffected by human development. Abundance, habitat use, and herd size information is therefore of interest for comparison with more developed areas.

We conducted a series of aerial surveys from July to December 1979 to examine the distribution and relative abundance of manatees and dolphins from Bayport, Hernando County (lat. 28°32′N, long. 82°39′W), Fla., south to Flamingo Ranger Station (ENP), Monroe County (lat. 25°08′N, long. 81°02′W), Fla.

METHODS

Surveys were conducted during five periods: 24 through 29 July, 6 through 11 and the 17th of

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[3]Hartman, D. S. 1974. Distribution, status, and conservation of the manatee in the United States. Report to U.S. Fish and Wildlife Service, National Fish and Wildlife Laboratory, Wash., D.C. National Technical Information Service PB 81 140725.

[4]Odell, D. K., and J. R. Reynolds III. 1980. Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Report to the U.S. Marine Mammal Commission, Wash., D. C. National Technical Information Service PB 80-197650.

[5]Irvine, A. B., M. D. Scott, and S. H. Shane. 1978. A study of the West Indian manatee, *Trichechus manatus*, in the Banana River and associated waters, Brevard County, Florida. U.S. Fish and Wildlife Service, National Fish and Wildlife Laboratory, Final Draft Contract Report to John F. Kennedy Space Center, NASA, Kennedy Space Center, FL 33899. Contract No. CC 63426A, KSC-DF-112.

[6]Shane, S. H. 1980. Manatees (*Trichechus manatus*) in Brevard County, Florida: Abundance, distribution and use of power plant effluents. Report to Florida Power and Light Co., P.O. Box 13100, Miami, FL 33101. Contract No. 61552-86540.

[7]Shane, S. H., and D. J. Schmidly. 1978. The population biology of the Atlantic bottlenosed dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. Report to U.S. Marine Mammal Commission, Wash., D.C. National Technical Information Service PB 283-393.

[8]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenosed dolphin, *Tursiops truncatus*, in-

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September, 2 through 8 October, 2 through 8 November, and 3 through 9 December 1979. Weather permitting, surveys were conducted on consecutive days in a chartered Cessna[9] 172 aircraft at an airspeed of about 160 km/h and an altitude of about 150 m. The final day of the September survey was postponed until 17 September because of adverse weather caused by Hurricane Frederic. The flight on 6 December was shortened, and flights scheduled for 7 and 8 December were cancelled due to inclement weather. The cancellation of those flights prevented December coverage of Charlotte Harbor and associated rivers, all of the Caloosahatchee and Orange Rivers, and the area from Estero Bay (Lee County) south to the Broad River (Monroe County) in ENP. The Whitewater Bay area of ENP was surveyed on 9 December 1979. After the July surveys, an extra survey day was added to the schedule, and daily coverage was redistributed to shorten flights in south Florida. Daily surveys lasted from 2 h 25 min to 6 h 21 min ($\bar{x}$ = 3 h 52 min).

Flights usually began between 0730 and 0800 h. The right door of the aircraft was removed to increase visibility on the 7 September flight and on all flights in subsequent months. One observer was seated in the right front and another in the left rear. Sighting locations of all manatees and dolphins were noted on charts of each earea by the forward observer. Comments were dictated into a cassette tape recorder, or noted directly on the chart. Calves were defined as small manatees or dolphins closely associating with larger animals of approximately twice their size (after Irvine and Campbell 1978). Dolphins or manatees within an arbitrary distance of about 100 m of conspecifics were counted as being in the same "herd" or group. Use of the term "herd" to describe social aggregations of dolphins is well established in the literature by Norris and Dohl (1980), but "herds" of manatees are not known to occur (Hartman 1979; Reynolds 1981).

Flight routes were marked on maps of the entire western Florida study area to facilitate consistent coverage on successive surveys. The routes were selected to cover probable manatee habitat (Hartman footnote 3; Irvine and Campbell 1978). Survey routes generally followed the 2 m bottom contour. The deepwater shipping channel was also surveyed in Tampa Bay. Pilots used the route maps to navigate, leaving the observers free to scan for animals. The plane deviated from the route only to investigate sightings and to count or photograph animals.

Areas surveyed included 1) bays and estuaries; 2) the Caloosahatchee River to the Ortona Lock in July and to Moore Haven on other surveys; 3) canals, bayous, rivers, and creeks (>1 m deep) up to 25 km inland; 4) the Intracoastal Waterway (ICW); 5) coastal areas to 0.5 km offshore, or to depths of about 2 m where shoals extended well offshore (Pasco and Hernando Counties).

Sighting locations on the flight record charts were categorized into three habitat types: 1) offshore: the Gulf of Mexico, 2) bay-estuary: bays, estuaries, and large rivers with direct access to the Gulf of Mexico, and 3) marsh-river: complex marsh habitats (Leatherwood and Platter[10]), inland bays (Monroe County), and narrow rivers. Using criteria from Remane and Schlieper (1971), salinity at each sighting location was subsequently classified as fresh (<0.5‰ salt), brackish (0.5 to 30‰ salt), or marine (>30‰ salt) based on available reports (E.P.A.[11]; Wang and Raney 1979[12]; U.S. Department of Commerce 1973; Weinstein et al. 1977; Schmidt and Davis 1978[13]). Offshore habitats were always categorized as marine, even though salinities in some areas might have been influenced by tide and freshwater runoff from recent storms. Relative survey effort was estimated as the percentage of total flight time in each habitat and salinity type.

Patterns of relative abundance and mean herd or group size were evaluated using chi-square and analysis of variance (ANOVA) procedures (Sokal and Rohlf 1969). Multiple comparisons among means were analyzed with Duncan's

cluding an evaluation of tagging techniques. Report to U.S. Marine Mammal Commission, Wash., D.C. National Technical Information Service PB 298 042.

[9]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[10]Leatherwood, S., and M. F. Platter. 1979. Aerial assessment of bottlenose dolphins off Alabama, Mississippi and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* assessment workshop, p. 49-86. Report to U.S. Marine Mammal Commission, Wash., D.C. National Technical Information Service PD 291 161.

[11]E.P.A. Water Quality Information Storage System (STQRET), 401 M. Street, SW., Wash., DC 20460.

[12]Wang, J. C. S., and E. C. Raney. 1971. Distribution and fluctuations in the fish fauna of the Charlotte Harbor Estuary, Florida. Charlotte Harbor Estuarine Studies. Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577.

[13]Schmidt, T. W., and G. E. Davis. 1978. A summary of estuarine and marine water quality information collected in Everglades National Park, Biscayne National Monument and adjacent estuaries from 1879 to 1977. U.S. National Park Service, South Florida Research Center, P.O. Box 279, Homestead, FL 33030. Report T-519.

Multiple Range Test (Steel and Torrie 1960). A square root transformation ($\sqrt{\text{herdsize} + 0.5}$) was applied to the counts to make them suitable for parametric analysis (Steel and Torrie 1960). Computations were performed with programs of the Statistical Analysis System (Helwig and Council 1979) at the University of Florida, Gainesville, Fla.

RESULTS

Manatees

Two hundred and ninety-seven groups of manatees, totaling 554 individuals, were observed during 121.8 survey hours (Fig. 1). Numbers sighted (Table 1) and average number of individuals per groups (Table 2) varied by county and month. Total numbers of manatees sighted increased from September to November, but the total per county consistently increased only in Monroe County. Total counts were not statistically compared among counties because habitat type, weather, and amount of survey area were not equivalent.

Ninety-four percent of the groups sighted consisted of one to four animals (Fig. 2). Group sizes were not observed with equal frequency, and more than half of the 297 sightings were of single animals ($P<0.005$; chi-square). However, 367 (66.2%) of the 554 manatees sighted were in groups. Pooled samples of all counties indicated that group size-frequency distributions did not vary significantly between months ($P>0.80$; chi-square).

Mean group size for the pooled sample of all sightings was 1.9 (SE = 0.12). A subset of data, including only those counties with sightings in each month (Monroe, Lee, and Sarasota Counties), was analyzed as a two-way ANOVA. This analysis provided no evidence of a month by county interaction ($P>0.85$), indicating that any pattern of monthly variation in group size was comparable for those three counties. Monthly variation in average group size, analyzed as a separate one-way ANOVA for each county, was significant ($P<0.05$) only in Hillsborough County, due to high December counts at warmwater effluents.

Numbers of manatees sighted were not proportional to the amount of survey time in each habitat type or salinity ($P<0.005$; chi-square). Pooled samples from all counties indicated that numbers of manatees sighted per month varied significantly by salinity and habitat ($P<0.0005$; chi-square). Except in December, substantially more manatees were sighted in marsh-river habitats than in other habitat types, and most were in brackish water (Table 3).

From 51 to 100 manatees, representing 54.3 to 75.7% of those sighted on July to November surveys and 58.5% overall, were observed in Monroe and Collier Counties (Table 1). Manatees were consistently sighted in Whitewater Bay, Chevalier Bay, and in the Lopez River (ENP, Monroe County), but the largest concentrations were found in Collier County from Marco Island to Chokoloskee. Manatees may have been overlooked if they were not near the surface or creating surface wakes or mud trails because of water turbidity (estimated visibility 0-0.5 m).

A maximum of two manatees per survey was sighted in Charlotte Harbor (Charlotte County; Fig. 1) and small numbers of manatees were consistently sighted in Pine Island Sound, Matlacha Pass, San Carlos Bay, in the lower reaches of the

TABLE 1.—Numbers of manatees and bottlenose dolphins observed, by county, during aerial surveys in western peninsular Florida from July to December 1979. C = calves.

	Manatees					Bottlenose dolphins				
County	July	Sept.	Oct.	Nov.	Dec.	July	Sept.	Oct.	Nov.	Dec.
Charlotte	4	5	6	0	[1]1	13+1C	22+1C	11+1C	1	[1]12+2C
Collier	41	49+2C	63+1C	49	([2])	9	20	11	29+1C	([2])
De Soto	0	0	0	0	([2])	0	0	0	0	([2])
Glades	0	0	0	1	([2])	0	0	0	0	([2])
Hendry	0	0	0	2+2C	([2])	0	0	0	0	([2])
Hernando	0	0	0	0	0	4	0	7	8	0
Hillsborough	16	3	0	0	47+3C	30+2C	17+2C	17	0	3
Lee	15	17+1C	7	26+1C	[1]12	34	37+1C	100+1C	32	[1]62+3C
Manatee	6	0	3	4	0	8+2C	6	44+3C	13	44+1C
Monroe	9+1C	10	20	48+3C	[1]28	15	35+2C	26+1C	66	[1]28+4C
Pasco	0	0	0	0	1	2	17+1C	27	119+3C	59+3C
Pinellas	0	0	0	0	7	56+1C	36+3C	39	73+2C	33+1C
Sarasota	2	6	11	14+1C	6	12+1C	60+4C	23+1C	6	9
Total	93+1C	90+3C	110+1C	144+7C	102+3C	183+7C	250+14C	305+7C	347+6C	250+14C

[1]Incomplete survey
[2]Not surveyed

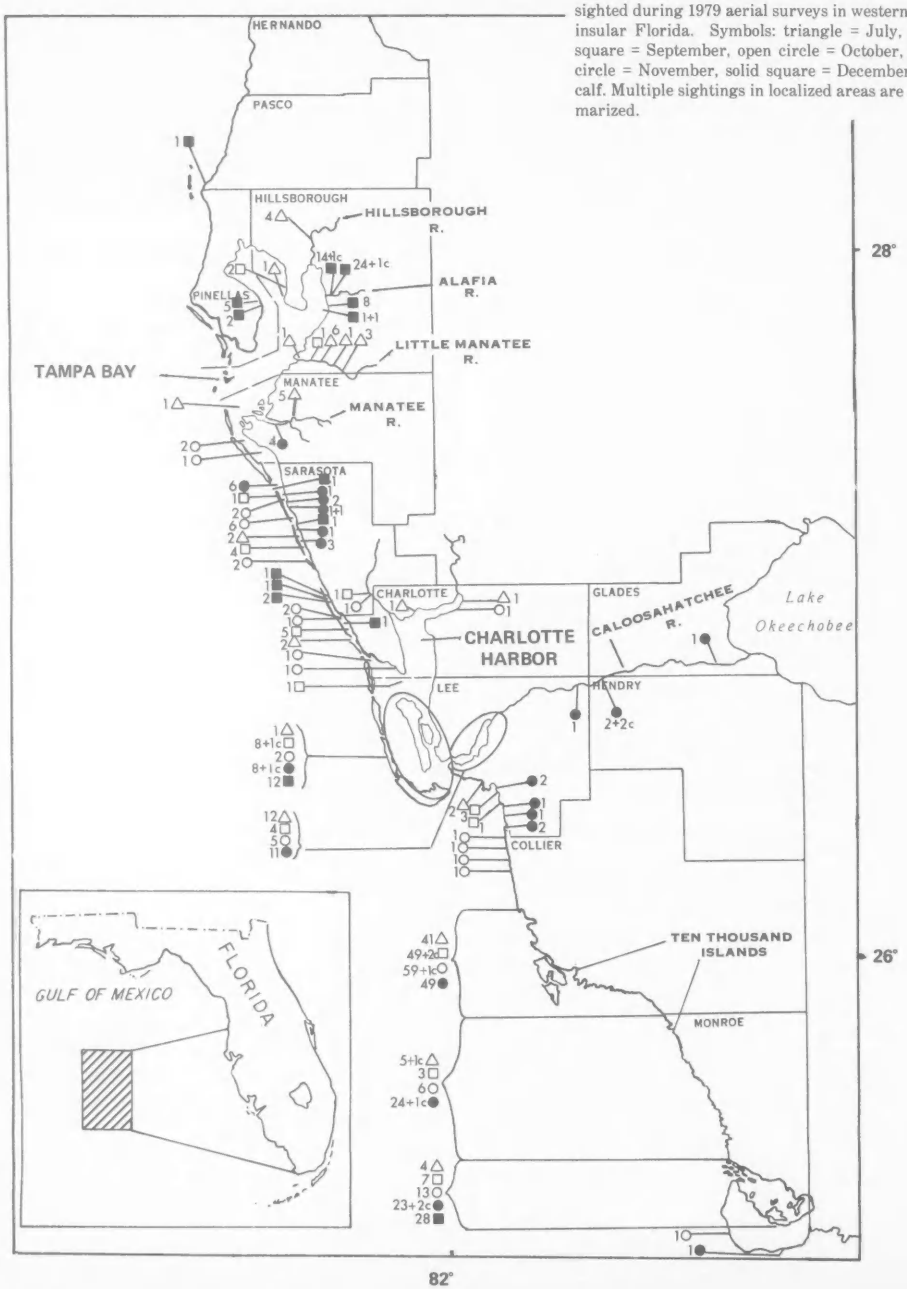

FIGURE 1.—Locations and numbers of manatees sighted during 1979 aerial surveys in western peninsular Florida. Symbols: triangle = July, open square = September, open circle = October, solid circle = November, solid square = December, c = calf. Multiple sightings in localized areas are summarized.

TABLE 2.—Average group or herd size of manatees and bottlenose dolphins sighted, by county, during aerial surveys of western peninsular Florida from July to December 1979.

	Manatees						Bottlenose dolphins					
County	July	Sept.	Oct.	Nov.	Dec.	Composite average	July	Sept.	Oct.	Nov.	Dec.	Composite average
Charlotte	1.3 (0.33;3)	5.0 (--;1)	1.2 (0.20;5)	—[2]	1.0 (--;1)	1.6 (0.4;10)	2.8 (0.86;5)	1.9 (0.40;12)	1.7 (0.57;7)	1.0 (--;1)	3.5 (1.50;4)	2.2 (0.33;29)
Collier	1.7 (0.27;24)	2.0 (0.38;25)	1.5 (0.16;42)	1.5 (0.15;33)	[3]	1.7 (0.11;12)	2.3 (0.63;4)	1.5 (0.33;13)	1.4 (0.26;8)	2.7 (0.84;11)	[3]	1.9 (0.30;36)
De Soto	—	—	—	—	[3]		—	—	—	—	[3]	—
Glades	—	—	—	1.0 (--;1)	[3]	1.0 (--;1)	—	—	—	—	[3]	—
Hendry	—	—	—	4.0 (--;1)	[3]	4.0 (--;1)	—	—	—	—	[3]	—
Hernando	—	—	—	—	—	—	4.0 (--;1)	—	7.0 (--;1)	1.3 (0.21;6)	—	2.4 (0.75;8)
Hillsborough	2.7 (0.84;6)	1.5 (0.50;2)	—	—	12.5 (4.94;4)	5.8 (2.11;12)	4.0 (0.57;8)	2.7 (1.13;7)	3.4 (2.40;5)	—	1.5 (0.50;2)	3.2 (0.66;22)
Lee	1.9 (0.30;8)	1.6 (0.24;11)	2.3 (0.88;3)	1.9 (0.32;14)	1.5 (0.19;8)	1.8 (0.14;44)	3.1 (0.68;11)	1.7 (0.24;22)	2.5 (0.36;41)	1.9 (0.41;17)	5.4 (1.45;12)	2.6 (0.27;103)
Manatee	3.0 (2.00;2)	—	1.5 (0.50;2)	4.0 (--;1)		2.6 (0.81;5)	3.3 (1.45;3)	1.5 (0.29;4)	4.7 (1.74;10)	2.6 (0.98;5)	15.0 (8.14;3)	4.8 (1.34;25)
Monroe	1.3 (0.16;8)	1.1 (0.11;9)	1.7 (0.36;12)	1.7 (0.26;31)	1.6 (0.34;18)	1.5 (0.14;78)	1.7 (0.33;9)	2.0 (0.58;19)	1.5 (0.15;18)	1.9 (0.22;35)	2.1 (0.65;15)	1.9 (0.18;96)
Pasco	—	—	—	—	1.0 (--;1)	1.0 (--;1)	2.0 (--;1)	4.5 (3.50;4)	27.0 (--;1)	20.3 (10.72;6)	10.3 (6.74;6)	12.8 (4.40;18)
Pinellas	—	—	—	—	3.5 (1.50;2)	3.5 (1.5;2)	2.7 (0.49;21)	4.3 (1.24;9)	3.9 (1.29;10)	5.0 (1.76;15)	4.3 (1.56;8)	3.9 (0.55;63)
Sarasota	2.0 (--;1)	2.0 (1.00;3)	2.8 (1.11;4)	2.5 (0.76;6)	1.2 (0.20;5)	2.1 (0.37;19)	2.2 (0.31;6)	5.8 (2.40;11)	4.8 (2.33;5)	1.2 (0.20;5)	2.3 (0.63;4)	3.7 (0.96;31)

[1]Standard error of the mean and *n* (sightings) in parentheses; -- = no value.
[2]No sightings.
[3]Not surveyed.

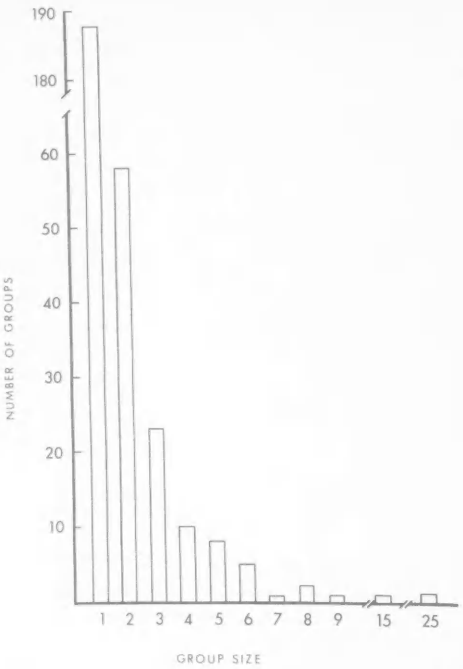

FIGURE 2.—Group size-frequency distribution of manatees sighted during aerial surveys from July through December 1979.

Caloosahatchee River, and in Estero Bay (Lee County). Manatees were sighted in the Upper Caloosahatchee River (Glades and Hendry Counties) only in November. Manatees were not sighted near the warmwater refuge in the Orange River, Lee County (Hartman footnote 3), but the area was not surveyed in December when ambient air and water temperatures were coldest.

A few manatees were consistently sighted between Charlotte Harbor and Tampa Bay. The animals were sighted in Lemon Bay, Roberts Bay, and Little Sarasota Bay, and were often near the channel of the ICW.

North of Sarasota County, manatees were primarily sighted in rivers emptying into Tampa Bay, including the Hillsborough, Alafia, Manatee, and Little Manatee Rivers. Our observations in Hillsborough and Manatee Counties may have been hampered in September by cloud cover and in October by turbid waters resulting from recent flooding.

Manatees were observed near warmwater refuges described by Hartman (footnote 3) only during the December flights. A total of 40 manatees was sighted at the two warm effluents of the Gibsonton Phosphate Plant in the Alfia River (Hillsborough County). Eight manatees were sighted in the Big Bend Power Plant effluent (Hillsborough County), and a cow and calf were observed just offshore of the effluent. Five manatees were observed at the P. L. Bartow Plant effluent (Pinellas County), and two manatees were observed near the intake canal. A single manatee was sighted in the intake canal of the Anclote Power Plant (Pasco County).

A maximum of three calves per county was sighted on any survey. Total percentage of calves sighted ranged from 0.9 to 4.9% on different surveys.

Bottlenose Dolphins

Four hundred and thirty-one herds, totaling 1,383 bottlenose dolphins, were observed. The total number of dolphins sighted increased from July to November, but fluctuated in most counties with no obvious trends (Table 1). Sightings were common in interior bays and rivers in ENP

TABLE 3.—Manatee and bottlenose dolphin sightings in different habitat-types and estimated salinities.

	Manatees						Bottlenose dolphins					
	Habitat-type			Salinity			Habitat-type			Salinity		
	Off-shore	Bay-estuary	Marsh-river	Fresh (<0.5‰)	Brackish (0.5-30‰)	Salt (>30‰)	Off-shore	Bay-estuary	Marsh-river	Fresh (<0.5‰)	Brackish (0.5-30‰)	Salt (>30‰)
Mean group or herd size (±SE)	1.29 (0.13)	2.38 (0.34)	1.69 (0.10)	1.93 (0.35)	1.85 (0.14)	1.93 (0.21)	4.79 (0.70)	2.65 (0.19)	1.92 (0.19)	0	2.19 (0.14)	3.97 (0.44)
No. of groups or herds	14	85	198	14	240	43	146	185	100	0	184	247
No. of animals (percent)	18 (3.2)	202 (36.5)	334 (60.3)	27 (4.9)	444 (80.1)	83 (15.0)	700 (50.7)	491 (35.5)	192 (13.9)	0	403 (29.1)	980 (70.9)
Percent of survey time	17.7	44.3	38.0	8.9	50.1	41.0	17.7	44.3	38.0	8.9	50.1	41.0

and well into Tampa Bay. In the Charlotte-Lee Counties area, dolphins were common in the Gulf of Mexico, around Pine Island, and occasionally in the lower Caloosahatchee River. Most coastal sightings were within 0.5 km of the beach.

Dolphin herd sizes were not sighted with equal frequency (Fig. 3); most sightings (56%) consisted of two or more animals ($P<0.005$; chi-square). Mean herd size for the pooled sample of all sightings was 3.2 dolphins/herd (SE = ±0.26). Effects of county and month on average herd size in counties with sightings in each month (Table 2) were analyzed as a two-way ANOVA. The county by month interaction was significant ($P<0.0005$), indicating that monthly variations in dolphin herd sizes were not comparable among counties. A separate one-way ANOVA for each county indicated that monthly variation in herd size was significant ($P<0.05$) only in Lee County, due to a high December mean. Pooled sightings from all counties indicated that herd size-frequency distributions varied significantly between months ($P<0.001$; chi-square), with fewer single dolphins and more large groups (>4) sighted in July and December.

Numbers of dolphins observed were not proportional to the amount of survey time in different habitats and salinities ($P<0.005$; chi-square). More animals were observed off the beach and in saltwater (Table 3), but monthly trends were not apparent. Dolphins were not sighted in freshwater. Pooled samples from all counties where sightings occurred indicated that numbers of dolphins sighted per month varied significantly by habitat and salinity ($P<0.001$). Most dolphins were sighted offshore in Pinellas and Sarasota Counties; more animals were in bay-estuary than in other habitats in Lee County; and most were in marsh-river habitats in Collier and Monroe Counties.

A maximum of 5.3% calves was observed during both the September and December surveys. A high of 12.5% calves was sighted in Monroe County in December, but this total may not be representative because relatively few dolphins were sighted in the area during the abbreviated surveys (Table 1).

DISCUSSION

Manatees are usually sighted in small groups when away from warmwater refuges. Eighty-six percent of the sightings during aerial surveys by Odell (1979) and 89% of the sightings by Hartman (1979) were of one to four manatees. Our results and those from other surveys (Hartman 1979; Odell 1979; Reynolds 1981) indicate that the greater percentage of manatees sighted are found in groups, but one is the most common group size. Although Hartman (1979) suggested that manatees are "essentially solitary," solitary manatees are nevertheless a minority of the total numbers sighted.

Odell (1979) sighted from 0 to 71 manatees

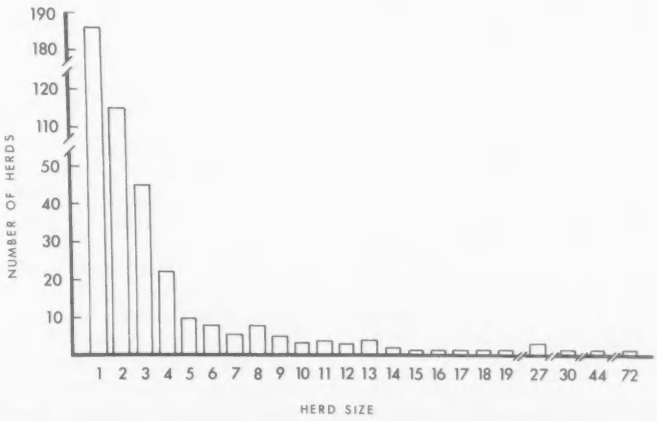

FIGURE 3.—Herd size-frequency distribution of bottlenose dolphins sighted during aerial surveys from July through December 1979.

during transect surveys conducted from July to December 1973 through 1976 in Monroe and Collier Counties. Hartman (footnote 3) sighted 45 manatees in Monroe and Collier Counties during a summer survey; Irvine and Campbell (1978) reported observing 163 manatees during a 1976 winter survey of the same area. Although abundance reports by different authors are not completely comparable because of variability among survey methodologies, results of our study clearly support previous reports that southwestern Florida is a center of manatee abundance (Moore 1951; Hartman footnote 3; Irvine and Campbell 1978).

Southerly shifts in the distribution of manatees in Florida during the fall were predicted by Moore (1951) and Hartman (footnote 3). Although total counts in Monroe and Collier Counties generally increased during fall surveys, the significance of this trend is unclear. Increased sightings may correlate with changes in manatee abundance, but could also indicate that the animals are for some reason more easily observed in that season. In any event, a southerly autumn shift in distribution cannot be conclusively shown based on our data.

The preponderance of manatee sightings in brackish water and marsh-river habitats occurred in the areas of Collier and Monroe Counties, which are characterized by that combination of habitat and salinity. Inland bays in ENP and Ten Thousand Islands area of Collier County were classified as "marsh-river" habitat because access to the Gulf of Mexico is restricted by relatively narrow or shallow channels. Although the survey results may be general indicators of habitat use, they should be viewed with some caution because all habitat types were not surveyed equally, and local salinities may have varied seasonally due to runoff from rainfall. Irvine and Campbell (1978) reported the relative frequencies of manatee sightings in fresh, brackish, and salt water as 19.1, 42.5, and 38.3%, respectively, during winter surveys, and 35.2, 34.9, and 29.6% during a summer survey of the entire state. In contrast, 80% of the manatees sighted in our surveys were in brackish water (Table 3).

The few sightings in Charlotte Harbor are noteworthy because manatees are often sighted by residents in this area (Moore 1951; Hartman footnote 3), and 36 manatees were counted in Charlotte Harbor during a summer aerial survey by Hartman (footnote 3). Manatee use of the Bartow and Anclote power plants has not been specifically reported, but two sightings mapped by Irvine and Campbell (1978) were at these plants.

We sighted few manatee calves (4.9% maximum per survey) compared with other surveys. Calves made up 5.2% of the animals sighted by Odell (1979) in Collier and Monroe Counties in 1973 through 1976, but during a 1976 winter survey of the same area, 10.4% of the manatees sighted were calves (Irvine and Campbell 1978). Leatherwood (1979) counted 9.9% calves in the Indian and Banana Rivers in eastern Florida, and Irvine and Campbell (1978) reported overall calf percentages of 9.6% in winter and 13.4% in summer from surveys of the entire state. Odell (1979) suggested that the tendency of calves to stay close to their mothers might result in fewer calf sightings in turbid waters, but this hypothesis has not been verified. Too few calves were sighted in our study to indicate seasonal reproductive trends.

The dolphin sightings are of particular interest due to the paucity of information on *T. truncatus* in nearshore areas of western peninsular Florida. The sightings were not analyzed for abundance and density estimates (see discussion by Leatherwood et al. 1978), because flight routes were designed to optimize manatee sightings and were not flown as straight lines. Our observations can, however, provide information on dolphin herd size and habitat use.

Average herd size (3.2 dolphins/herd) was considerably smaller than herd sizes reported from other aerial surveys in nearshore areas. In coastal waters of Alabama, Mississippi, and Louisiana, herd sizes averaged 25.2 dolphins with herd size in marshlands averaging 16.7 (Leatherwood and Platter footnote 10). Subgroups contained a mean of 5 dolphins in sounds and 3.8 dolphins in marshes (Leatherwood and Platter footnote 10). Barham et al. (1980) reported that herd sizes averaged 6.95 dolphins in Texas, and Leatherwood (1979) reported herds averaging 8.20 dolphins in eastern Florida. In primarily estuarine areas of western Florida, group size (equivalent to herd size as used here) was 4.8 dolphins/group (Irvine et al. 1981). Differences between observed herd sizes have been attributed to the influence of geography and habitat on dolphin groups structure (Leatherwood and Platter footnote 10), with largest groups found offshore (Wells et al. 1980). However, criteria for defining "herds" or "subgroups" are rarely reported, and could influence differ-

ences in reported results. During our surveys we often encountered several herds within a few kilometers of each other, after not seeing dolphins for distances of 20 km or more. Although such assemblages may have been dispersed subgroups of a larger herd, they did not meet our arbitrary criteria for defining a "herd." Our spatial definition of herd may be unsatisfactory if bottlenose dolphins, like some other cetaceans, maintain acoustic contact over many kilometers (Payne and Webb 1971). Acoustic contact among free ranging groups of *T. truncatus*, however, has not been demonstrated, and we know of no more appropriate basis for defining herds from aerial sightings.

The proportion of dolphin calves noted during our surveys (5.3%) is low when compared with other reports. Leatherwood (1979) observed 8.1-10.1% calves during aerial surveys in eastern Florida in August, while Irvine et al. (footnote 8) reported a maximum of 11% from May to July during surface surveys near Sarasota, Fla. Shane and Schmidly (footnote 7) noted that calves constituted 7.6% of all dolphin sightings during surface surveys near Port Aransas, Tex., and Barham et al. (1980) sighted 9.3% calves from the air in the same area. Leatherwood[14] observed 7.7% calves in 1974 and 7.9% calves in 1975 near the mouth of the Mississippi River. Our calf counts may be lower because we only counted very small animals; calves may grow to 2 m long within the first year (Leatherwood footnote 14) and therefore large calves may not have been distinguished as such.

SUMMARY AND CONCLUSIONS

Most of the manatees (58.5%) were located in the Everglades National Park (Monroe County) and Ten Thousand Islands (Collier County) areas, and most (80.1%) were in brackish water. Because these areas are relatively undisturbed by human development, they have great value as locations to protect and study the endangered manatee.

Dolphins were well dispersed in the survey area. Fifty-one percent were sighted in the Gulf of Mexico, 49% were in brackish water, and none were located in freshwater.

Seasonal movement patterns and reproductive trends based on calf sightings of both dolphins and manatees are unclear. While the survey results are valuable as indicators of relative abundance, they are not useful to estimate total abundance because the percentage of animals not observed is unknown.

[14]Leatherwood, S. 1977. Some preliminary impressions on the numbers and social behavior of free swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the northern Gulf of Mexico. *In* S. H. Ridgway and K. W. Benirshke (editors), Breeding dolphins: Present status, suggestions for the future, p. 143-167. National Technical Information Service PB 273 673.

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NOTES

EFFECT OF SEASON AND LOCATION ON THE RELATIONSHIP BETWEEN ZOOPLANKTON DISPLACEMENT VOLUME AND DRY WEIGHT IN THE NORTHWEST ATLANTIC[1]

Biomass or "standing stock" is a routinely measured index of abundance for studies of the interactions between trophic levels in the oceanic food web. Zooplankton biomass is usually reported as quantity of zooplankton per unit volume of water. Measures of quantity currently in use include displacement volume (Frolander 1957; Sutcliffe 1957; Yentsch and Hebard 1957; Tranter 1960; Ahlstrom and Thrailkill 1963), wet weight (Nakai and Honjo 1962), dry weight (Lovegrove 1966), and carbon (Curl 1962; Platt et al. 1969). These measures can be applied to a species at a specific developmental stage, to the entire population, or to all members of the community combined. Carbon and dry weight have been considered preferable because variability caused by interstitial and intracellular water is eliminated by either technique (Ahlstrom and Thrailkill 1963). They are not, however, practical measures in some investigations because specialized equipment is required and the techniques' destructive nature prevents further analysis of the sample. Measurement of displacement volume and wet weight are nondestructive, rapid, and use simple techniques which provide indexes of abundance, but do measure total matter, including water.

As an alternative, conversion factors or tables of "equivalents" have been used to transform displacement volume or wet weight into carbon or dry weight (Bsharah 1957; Menzel and Ryther 1961; Platt et al. 1969; Bé et al. 1971; Le Borgne 1975; Wiebe et al. 1975). However, plankton samples represent aggregations of organisms at a particular time and place which change according to season, geographical location, and local environmental conditions. For these reasons, and because many conversion factors were calculated with data produced by outdated techniques, the accuracy of interconversions between biomass measures has been questioned (Lovegrove 1966; Platt et al. 1969; Beers 1974). Recently, Wiebe et al. (1975) provided conversion factors based on data collected from different oceanic areas over several years in order to account for seasonal and geographical variation in samples.

This study explores whether a conversion equation based on data from numerous samples collected in contiguous areas during different seasons can account for sample variability and more accurately convert between biomass measures than equations derived from smaller and smaller subsets of data. Unlike previous studies, an intense sampling strategy provided the means to derive equations to convert between displacement volume and dry weight for samples from both broad and restricted geographic areas and for different seasons. Interconversion accuracy was verified with subsequent samples by comparing estimated values with field measurements. In addition, the relative variability and the values of both measures were compared in order to determine which index is more useful for these types of studies.

Materials and Methods

Plankton samples were collected by the National Marine Fisheries Service Northeast Fisheries Center in conjunction with the Marine Resources Monitoring Assessment and Prediction (MARMAP) program (Sherman 1980). Sampling was conducted six times a year in 1977 and 1978 off the northeast coast of the United States in three adjacent areas: Gulf of Maine (GOM), Georges Bank (GB), and Southern New England (SNE). Sampling locations are shown in Figures 1 and 2. Paired 61 cm diameter bongo samplers fitted with 0.505 mm and 0.333 mm mesh nets were towed obliquely through the water column at a speed of 1.5-2.0 kn. Maximum sampling depth was 200 m or 5 m from the bottom in shallower areas, and tow duration was 5-15 min. A flowmeter was strung inside the bongo frame to measure the volume of water filtered. Plankton samples from the 0.333 mm mesh nets were used in this analysis. Samples were preserved in 5% buffered Formalin[2] for at least 6 mo before anal-

[1]MARMAP Contribution MED/NEFC 81-8.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

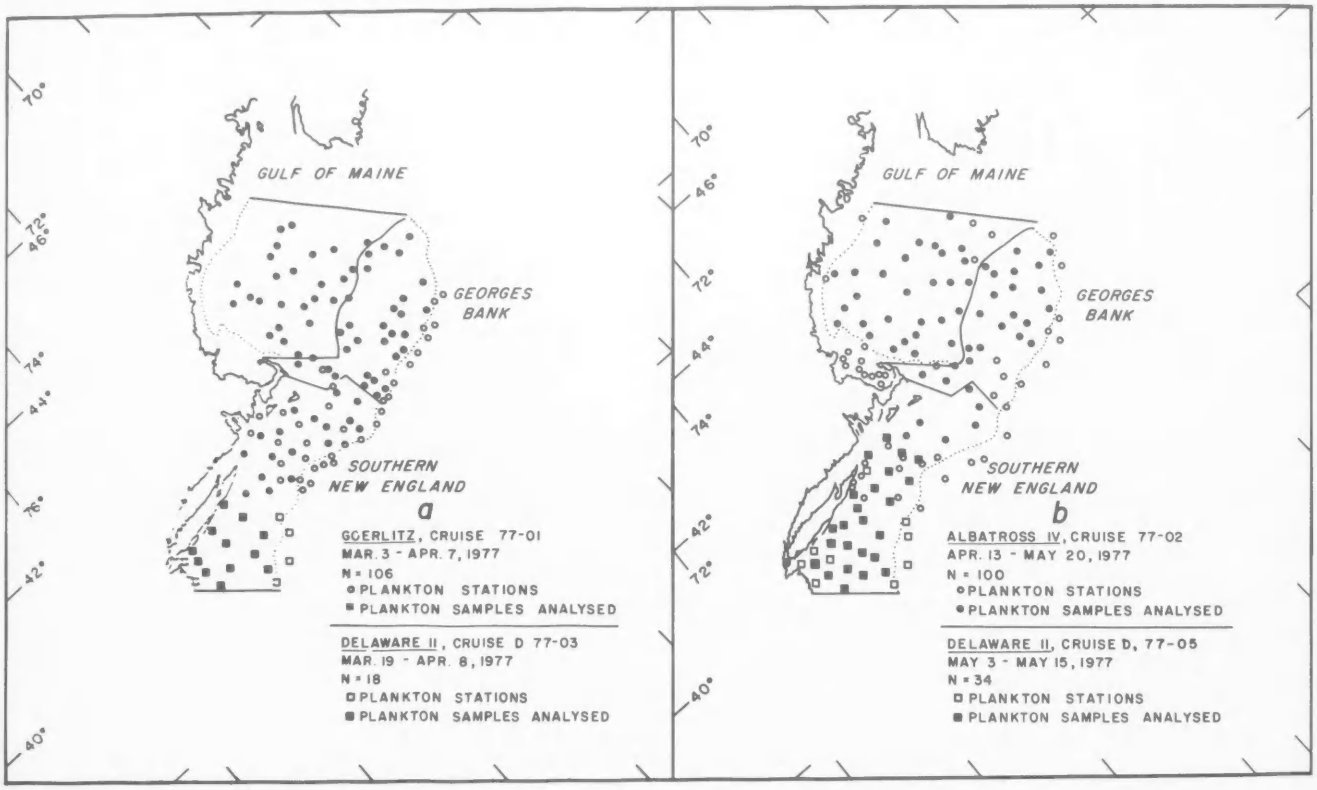

FIGURE 1.—Sampling locations and cruise numbers from the six seasonal MARMAP surveys for 1977.

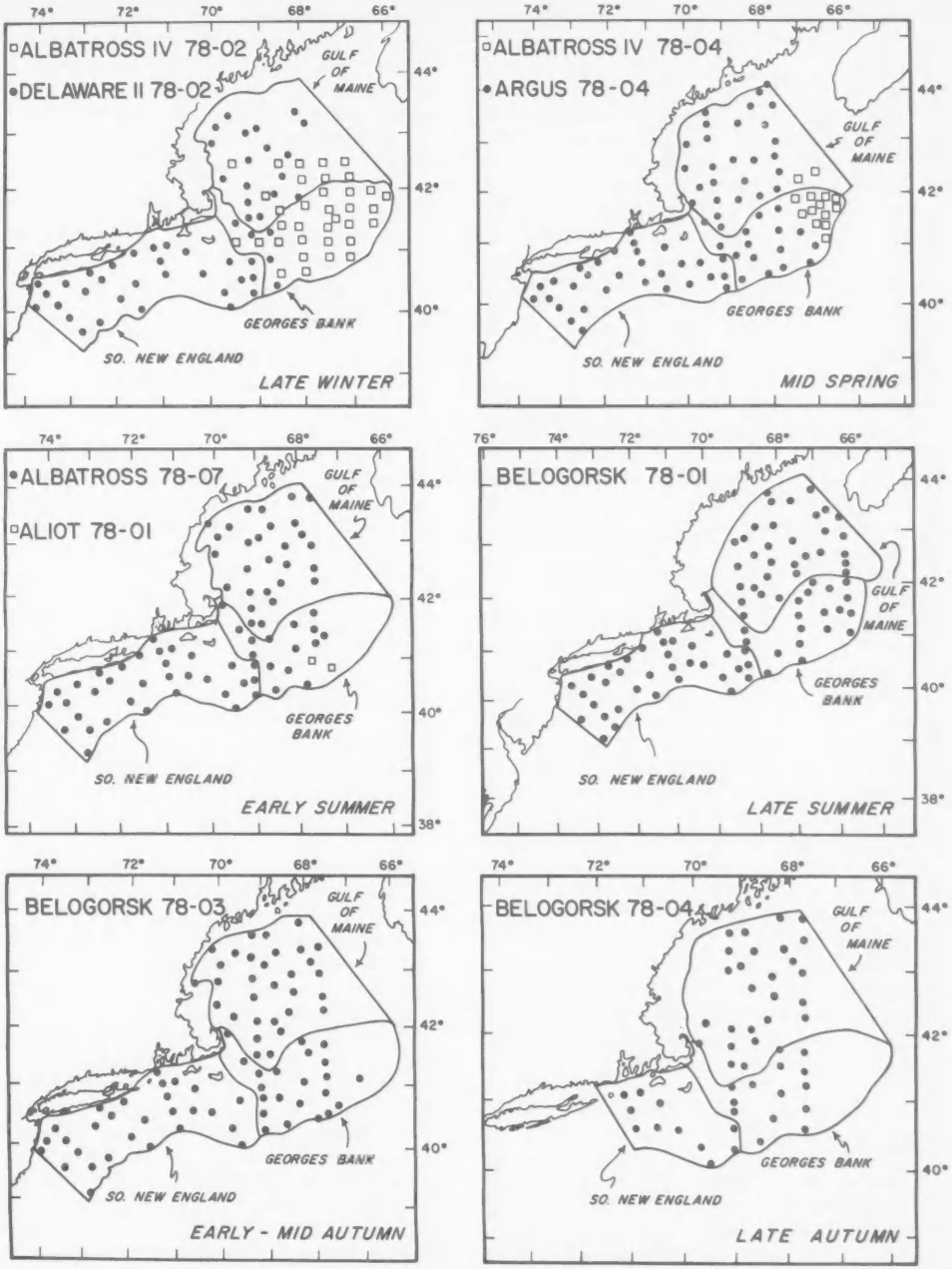

FIGURE 2.—Sampling locations and cruise numbers from the six seasonal MARMAP surveys for 1978.

ysis, sufficient time for the plankton to reach equilibrium volume and weight (Steedman 1976).

In the laboratory, displacement volumes were determined by using the technique outlined by Ahlstrom and Thrailkill (1963), with slight modifications. All organisms larger than 2.5 cm and nonplanktonic matter, i.e., small adult fishes, juvenile fishes, and seaweed, were removed prior to pouring the sample into a 1 l graduated cylinder, with 1 ml increments. After recording the volume, the sample was poured into a cone of 0.253 mm mesh suspended over a second graduated cylinder, and allowed to drain until the interval between drops was 15 s. The water volume was recorded. The difference between readings was recorded as the displacement volume. Dry weight was measured using the procedure outlined by Lovegrove (1966). Samples were dried at 60°C to a constant weight (2-5 d); a weight loss of 1 mg or less was considered constant. Samples were weighed to 0.01 mg on an analytical microbalance. Before analysis, all values were expressed as ml or gm/100 m^3 of water filtered and logarithmically transformed (base 10).

The geometric mean (GM) regression was used to express the relationship between displacement volume and dry weight because it is applicable to short series of measurements that have moderate or large variability, where the nature of error sources in the measurements is primarily natural, when compared with measurement error (Ricker 1973). The convention of using the GM regression for relating pairs of biomass measures was introduced by Wiebe et al. (1975), where a more detailed discussion of the theoretical and mathematical considerations of the GM regression as it applies to biomass measures is presented.

Using samples collected in 1977, conversion equations for displacement volume to dry weight were calculated using GM regressions for groups of measurements divided according to station and/or time of sampling as follows:

1) General: All measurements regardless of location or season (1).

2) Area: All measurements from a distinct oceanic region throughout the year (3).

3) Seasonal: Measurements within an area for a particular season (18).

Individual displacement volume readings from 1978 samples were converted to dry weight using each type of conversion equation. The predictive accuracy of the different equations was calculated by measuring the difference between the estimated and the directly measured dry weight, and expressing this difference as a percentage of the latter. The absolute values of the percent deviations for each conversion factor were then averaged for each group of seasonal and area-specific samples to determine which equation was most accurate. This method for evaluating different conversion factors was used instead of comparing differences between measured and estimated means because of the cancelling effect very high or low estimates would have on each other.

Results

A strong linear relationship exists between zooplankton displacement volume and dry weight (Table 1). Slopes of the GM regression lines were significantly different from zero ($P<0.001$), and correlation coefficients were high (0.885-0.977) for all lines within each class. The range of slope and elevation values for the 18 seasonal equations was significantly wide ($P<0.05$) to conclude that the different lines were not expressing the same biomass relationship. It was hypothesized that from among these regression lines there might exist discrete groups of significantly similar lines which could be combined to describe a fourth category of conversion equations. A Neuman-Keuls multiple range test (Zar 1974) pinpointed lines which differed significantly ($P<0.05$) in slope and/or elevation, but other lines could not be accurately assigned to distinct groups because of overlapping similarities. Increasing the amount of data might yield more acceptable conclusions, but it is more likely that these results reflect a gradient of changing trophic conditions which gradually alter the biomass relationship from season to season.

The seasonal class of conversion equations yielded significantly ($P<0.05$) more accurate estimates than either the general or areal equations. For the 18 groups of seasonal and areal samples collected in 1978, predicted dry weights on the average deviated 15.98% (range: 2.31-34.4%) from the actual values using the seasonal equations, as opposed to 29.27% (range: 12.62-66.34%) and 31.4% (range: 15.90-53.45%) for the areal and general equations, respectively. However, for certain seasons, the appropriate regression equation did not accurately convert dis-

TABLE 1.—Geometric mean regression equations calculated from 1977 displacement volume (DV) and dry weight (DW) measures for each area by season, each individual area, and for all values combined. Also included is the equation for phytoplankton-dominated stations.

Area/season	Regression equation	N	r	Variance of slope
Southern New England				
I Late winter-early spring	Log (DW) = −1.079 + 0.963 Log (DV)	27	0.951	0.00348
II Midspring	Log (DW) = −1.235 + 1.022 Log (DV)	30	0.900	0.00706
III Late spring	Log (DW) = −1.663 + 1.312 Log (DV)	30	0.956	0.00532
IV Midsummer	Log (DW) = −1.803 + 1.382 Log (DV)	34	0.890	0.0123
V Midautumn	Log (DW) = −1.190 + 0.976 Log (DV)	27	0.907	0.00672
VI Late autumn	Log (DW) = −1.245 + 1.006 Log (DV)	20	0.961	0.00476
All seasons	Log (DW) = −1.226 + 1.138 Log (DV)	168	0.943	0.000106
Georges Bank				
I Late winter-early spring	Log (DW) = −1.182 + 1.045 Log (DV)	28	0.885	0.00902
II Midspring	Log (DW) = −1.328 + 1.114 Log (DV)	23	0.929	0.00811
III Late spring	Log (DW) = −1.405 + 1.184 Log (DV)	27	0.930	0.00757
IV Midsummer	Log (DW) = −1.552 + 1.274 Log (DV)	21	0.898	0.0166
V Early autumn	Log (DW) = −1.622 + 1.296 Log (DV)	18	0.949	0.0104
VI Late autumn	Log (DW) = −1.210 + 1.091 Log (DV)	20	0.914	0.0111
All seasons	Log (DW) = −1.308 + 1.127 Log (DV)	137	0.954	0.000823
Gulf of Maine				
I Early spring	Log (DW) = −1.161 + 1.142 Log (DV)	13	0.960	0.00922
II Midspring	Log (DW) = −1.347 + 1.223 Log (DV)	21	0.954	0.00593
III Late spring	Log (DW) = −1.170 + 1.145 Log (DV)	27	0.947	0.00548
IV Midsummer	Log (DW) = −1.470 + 1.377 Log (DV)	28	0.966	0.00476
V Midautumn	Log (DW) = −1.201 + 1.242 Log (DV)	23	0.977	0.00339
VI Late autumn	Log (DW) = −1.747 + 1.514 Log (DV)	30	0.932	0.0108
All seasons	Log (DW) = −1.311 + 1.257 Log (DV)	142	0.963	0.00290
All areas				
Every season	Log (DW) = −1.383 + 1.207 Log (DV)	447	0.925	0.000484
Phytoplankton stations	Log (DW) = −1.481 + 1.016 Log (DV)	20	0.962	0.00910

placement volume to dry weight. It was found that a change in the biomass relationship occurred between years in the six seasons that predictive accuracy was lowest. This was determined by calculating regressions with 1978 data (Table 2) and comparing them with the corresponding 1977 seasonal equations. Year-to-year differences ($P<0.05$) in slope and/or elevation were evident for the following: GB early-mid-autumn, GB late autumn, GOM mid-late summer, GOM midautumn, SNE late winter, and SNE late spring-early summer. After perusal of sample contents, sampling dates, and sample species abundance, it was apparent that year-to-year changes in these factors were correlated with the 1977-78 differences in the regression equations mentioned above (Tables 3-5).

For those areas where no change in the relationship between displacement volume and dry weight occurred between years, data was com-

TABLE 2.—Geometric mean regression equations derived from 1978 displacement volume (DV) and dry weight (DW) values for each area by season and for samples with abundant siphonophore fragments.

Area/season	Regression equation	N	r	Variance of slope
Southern New England				
VII Late winter	Log (DW) = −0.795 + 0.725 Log (DV)	21	0.903	0.00810
VIII Midspring	Log (DW) = −1.287 + 1.088 Log (DV)	25	0.960	0.00620
IX Early summer	Log (DW) = −1.939 + 1.541 Log (DV)	30	0.969	0.00980
X Midsummer	Log (DW) = −1.802 + 1.388 Log (DV)	19	0.939	0.01900
XI Midautumn	Insufficient Data			
XII Late autumn	Log (DW) = −1.266 + 1.045 Log (DV)	10	0.927	0.0219
Georges Bank				
VII Late winter	Log (DW) = −1.229 + 1.095 Log (DV)	23	0.964	0.00941
VIII Midspring	Log (DW) = −1.515 + 1.238 Log (DV)	20	0.990	0.00260
IX Early summer	Log (DW) = −1.416 + 1.186 Log (DV)	16	0.900	0.0123
X Late summer	Log (DW) = −1.079 + 0.956 Log (DV)	18	0.881	0.0156
XI Midautumn	Log (DW) = −1.349 + 1.070 Log (DV)	20	0.945	0.00941
XII Late autumn	Log (DW) = −1.509 + 1.215 Log (DV)	14	0.950	0.0129
Gulf of Maine				
VII Late winter	Log (DW) = −1.158 + 1.148 Log (DV)	21	0.913	0.0219
VIII Midspring	Log (DW) = −1.137 + 1.085 Log (DV)	25	0.947	0.00865
IX Early summer	Log (DW) = −0.949 + 1.042 Log (DV)	27	0.927	0.00846
X Late summer	Log (DW) = −1.079 + 1.089 Log (DV)	22	0.949	0.00846
XI Midautumn	Log (DW) = −1.343 + 1.304 Log (DV)	24	0.957	0.0129
XII Late autumn	Log (DW) = −1.454 + 1.349 Log (DV)	20	0.875	0.0353
Siphonophore samples	Log (DW) = −0.975 + 0.773 Log (DV)	15	0.969	0.00397

TABLE 3.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Southern New England area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A

Season	Regression equation	N	r	Variance of slope
Late winter	Log (DW) = −0.795 + 0.725 Log (DV)	21	0.903	0.00810
Early spring	Log (DW) = −1.079 + 0.963 Log (DV)	27	0.951	0.00348
Midspring	Log (DW) = −1.103 + 0.929 Log (DV)	55	0.929	0.00348
Late spring	Log (DW) = −1.663 + 1.312 Log (DV)	30	0.956	0.00532
Early summer	Log (DW) = −1.939 + 1.541 Log (DV)	30	0.969	0.00980
Midsummer	Log (DW) = −1.795 + 1.379 Log (DV)	53	0.900	0.00757
Midautumn	Log (DW) = −1.190 + 0.976 Log (DV)	27	0.907	0.00672
Late autumn	Log (DW) = −1.251 + 1.109 Log (DV)	30	0.956	0.00360

B

Late winter		Early spring		Midspring		Late spring	
Copepoda	88.6	Copepoda	88.2	Copepoda	91.5	Copepoda	88.4
P. minutus	(87.8)	*P. minutus*	(75.1)	*C. finmarchicus*	(55.3)	*P. minutus*	(44.3)
C. finmarchicus	(6.2)	*C. finmarchicus*	(8.5)	*P. minutus*	(28.8)	*C. finmarchicus*	(37.2)
C. typicus	(3.0)	*T. longicornus*	(6.2)	*M. lucens*	(3.0)	*T. longicornus*	(11.7)
Chaetognatha	8.6	*C. typicus*	(5.4)	*A. longiremus*	(1.9)	*M. lucens*	(2.3)
		Cirripedia	9.6	*C. typicus*	(1.3)	Chaetognatha	6.3
				Chaetognatha	4.2	Cladocera	3.0
				Cladocera	1.4		

Early summer		Midsummer		Midautumn		Late autumn	
Copepoda	91.3	Copepoda	66.2	Copepoda	75.6	Copepoda	91.8
P. minutus	(33.9)	*C. typicus*	(59.8)	*C. typicus*	(70.1)	*C. typicus*	(60.6)
C. finmarchicus	(27.8)	*C. finmarchicus*	(19.8)	*A. clausi*	(5.1)	*P. parvus*	(15.3)
C. typicus	(19.0)	*P. minutus*	(5.2)	*A. tonsa*	(4.0)	*P. minutus*	(11.0)
T. longicornus	(11.6)	*M. lucens*	(3.1)	*P. minutus*	(3.4)	Chaetognatha	5.5
M. lucens	(1.2)	Cladocera	23.6	*P. parvus*	(3.2)		
Chaetognatha	7.8	Chaetognatha	4.5	*C. minor*	(2.2)		
		Thaliacea	1.7	Cladocera	21.3		
		Amphipoda	1.6	Chaetognatha	1.0		

TABLE 4.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Georges Bank area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A

Season	Regression equation	N	r	Variance of slope
Late winter-early spring	Log (DW) = −1.195 + 1.059 Log (DV)	39	0.908	0.00518
Midspring	Log (DW) = −1.324 + 1.119 Log (DV)	37	0.989	0.00372
Late spring-early summer	Log (DW) = −1.360 + 1.159 Log (DV)	40	0.954	0.00314
Midsummer-late summer	Log (DW) = −1.403 + 1.176 Log (DV)	36	0.891	0.00828
Early autumn	Log (DW) = −1.662 + 1.296 Log (DV)	18	0.949	0.0104
Midautumn	Log (DW) = −1.349 + 1.070 Log (DV)	20	0.945	0.00941
Late autumn (1977)	Log (DW) = −1.210 + 1.091 Log (DV)	20	0.914	0.0111
Late autumn (1978)	Log (DW) = −1.509 + 1.215 Log (DV)	14	0.950	0.0129

B

Late winter-early spring		Midspring		Late spring-early summer		Midsummer	
Copepoda	80.7	Copepoda	89.7	Copepoda	76.6	Copepoda	89.3
P. minutus	(55.6)	*C. finmarchicus*	(79.8)	*C. finmarchicus*	(42.8)	*C. typicus*	(53.1)
C. finmarchicus	(37.1)	*P. minutus*	(16.9)	*P. minutus*	(36.1)	*C. hamatus*	(16.6)
C. typicus	(2.6)	*M. lucens*	(2.5)	*C. hamatus*	(11.7)	*C. finmarchicus*	(10.2)
M. lucens	(1.8)	Chaetognatha	2.3	*C. typicus*	(5.1)	*P. minutus*	(8.9)
Chaetognatha	6.9	Ostracoda	1.5	*M. lucens*	(1.5)	*P. parvus*	(5.6)
Cirripedia	4.9	Cirripedia	1.3	*T. longicornus*	(1.3)	*M. lucens*	(3.7)
Amphipoda	4.8	Amphipoda	1.1	Chaetognatha	6.7	Chaetognatha	4.9
Pelecypoda	1.7			Coelenterata	5.6	Cladocera	1.8
				Cladocera	4.1		
				Decapoda	3.1		

Early autumn		Midautumn		Late autumn (1977)		Late autumn (1978)	
Copepoda	95.1	Copepoda	94.5	Copepoda	86.6	Copepoda	89.8
C. typicus	(50.1)	*C. typicus*	(64.6)	*C. typicus*	(57.0)	*C. typicus*	(51.1)
P. minutus	(19.8)	*C. finmarchicus*	(10.2)	*P. minutus*	(28.0)	*P. parvus*	(19.9)
C. hamatus	(18.4)	*C. hamatus*	(8.7)	*C. finmarchicus*	(4.3)	*C. finmarchicus*	(11.0)
C. finmarchicus	(2.5)	*P. parvus*	(5.7)	*C. hamatus*	(3.8)	*P. minutus*	(7.9)
M. lucens	(2.0)	*P. minutus*	(5.6)	*P. parvus*	(2.2)	*C. hamatus*	(6.1)
P. parvus	(1.9)	*M. lucens*	(1.3)	*M. lucens*	(1.7)	Chaetognatha	8.7
Pelecypoda	1.7	Chaetognatha	2.3	Pelecypoda	6.9		
Chaetognatha	1.3	Amphipoda	1.4	Chaetognatha	5.5		

TABLE 5.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Gulf of Maine area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A

Season	Regression equation	*N*	*r*	Variance of slope
Late winter-early spring	Log (DW) = −1.168 + 1.156 Log (DV)	25	0.956	0.00504
Midspring	Log (DW) = −1.169 + 1.106 Log (DV)	37	0.954	0.00314
Late spring-early summer	Log (DW) = −1.035 + 1.080 Log (DV)	47	0.949	0.00260
Midsummer	Log (DW) = −1.470 + 1.377 Log (DV)	28	0.966	0.00476
Late summer	Log (DW) = −1.079 + 1.089 Log (DV)	22	0.949	0.00846
Midautumn (1977)	Log (DW) = −1.201 + 1.242 Log (DV)	23	0.977	0.00339
Midautumn (1978)	Log (DW) = −1.343 + 1.304 Log (DV)	24	0.957	0.0129
Late autumn	Log (DW) = −1.576 + 1.419 Log (DV)	44	0.935	0.00608

B

Late winter-early spring		Midspring		Late spring-early summer		Midsummer	
Copepoda	96.3	Copepoda	93.5	Copepoda	94.0	Copepoda	97.5
C. finmarchicus	(63.7)	*C. finmarchicus*	(86.7)	*C. finmarchicus*	(83.5)	*C. finmarchicus*	(79.9)
M. lucens	(18.9)	*P. minutus*	(8.0)	*P. minutus*	(10.3)	*P. minutus*	(10.0)
P. minutus	(13.6)	*M. lucens*	(5.0)	*M. lucens*	(4.6)	*M. lucens*	(4.2)
Oithona sp.	(1.7)	Amphipoda	5.0	*A. longiremis*	(1.1)	*C. typicus*	(4.2)
Amphipoda	1.3			Cladocera	4.8	*A. longiremis*	(1.3)
						Cladocera	1.1

Late summer		Midautumn (1977)		Midautumn (1978)		Late autumn	
Copepoda	99.2	Copepoda	99.0	Copepoda	98.9	Copepoda	99.1
C. finmarchicus	(47.3)	*C. finmarchicus*	(51.3)	*C. typicus*	(39.1)	*C. typicus*	(37.0)
C. typicus	(42.0)	*C. typicus*	(29.3)	*C. finmarchicus*	(34.6)	*C. finmarchicus*	(28.3)
P. minutus	(7.7)	*P. minutus*	(11.4)	*P. minutus*	(17.9)	*P. minutus*	(21.4)
		M. lucens	(3.5)	*A. longiremis*	(1.5)	*P. parvus*	(4.7)
		P. parvus	(2.6)	*P. parvus*	(1.3)	*M. lucens*	(4.5)
						A. longiremis	(1.1)

bined and a new regression equation calculated. These equations, and the equations showing significant differences between years, are the recommended equations for conversion between the biomass measures (Tables 3-5). Choice of which regression to use should be based on area, season, and species composition. Confidence limits can be calculated for any predicted dry weight or displacement volume by using the method outlined by Ricker (1973) or Wiebe et al. (1975). A listing of values for predicting dry weights and displacement volumes within 95% confidence limits is given in Table 6.

The limitations of the method for the area under study are as follows. The presence in samples of organisms such as salps, jellyfish, and doliolids, which have a high displacement volume to dry weight ratio due to a greater retention of intracellular water, can significantly affect the accuracy of dry weight estimates (Wiebe et al. 1975). This was also observed in our data, but only on rare occasions were these organisms encountered. Chaetognaths were also mentioned by Wiebe et al. as organisms that could alter the biomass relationship. Since they are common, but not dominant, components of the plankton throughout the year in our sampling areas, the seasonal regressions account for their continuous presence and are therefore applicable to samples where they are present. This study revealed two additional situations in which sample composition caused a deviation in the biomass relationship. Twenty samples collected during late winter 1977 from the GOM and GB contained high concentrations of diatoms, primarily *Rhizosolenia* sp. and *Thalassiosira* sp., and microzooplankton not normally captured by 0.333 mm mesh nets. The samples resembled thick "pea soup" and many hours were required for draining in order to obtain a displacement volume reading. Since their dry weight to displacement volume ratios were very low compared with other samples collected during the same period, the samples were eliminated from the general analysis and a separate regression calculated ($r = 0.962$) for them (Table 1). The second situation was observed in autumn 1978 when the siphonophore population increased dramatically, especially off SNE and in the GOM. Since these delicate colonial aggregations are easily fragmented during collection, their abundance could not be measured quantitatively. For these samples, displacement volume to dry weight ratios were disproportionally high because of the intracellular water retained by their nectophores. The regression line calculated with data only from siphonophore-dominated samples was significantly different ($P<0.05$) in both

TABLE 6.—Values needed to calculate 95% confidence limits for predicted dry weights (DW) and displacement volumes (DV) from the equations in Tables 3-5. For an explanation of symbols and the methods used, one should consult Ricker (1973) or Wiebe et al. (1975).

Area/season	Prediction of DW				Prediction of DV		
	t_{95}	$\bar{X}'$	$\Sigma x'^2$	$Sy'x'^2$	$\bar{Y}'$	$\Sigma y'^2$	$Sx'y'^2$
Southern New England							
Late winter	2.05	1.329	4.384	0.0156	0.775	4.067	0.0168
Early spring	2.08	0.945	1.894	0.0154	−0.110	0.996	0.0292
Midspring	2.01	1.598	8.156	0.0281	0.478	9.250	0.0248
Late spring	2.04	1.915	2.025	0.0107	0.850	3.484	0.00622
Early summer	2.04	1.683	0.694	0.00671	0.655	1.651	0.00282
Midsummer	2.01	1.706	2.614	0.0205	0.577	4.973	0.0108
Midautumn	2.05	1.334	1.147	0.00780	0.117	1.092	0.0081
Late autumn	2.05	1.347	1.588	0.00568	0.121	1.648	0.00545
Georges Bank							
Late winter-early spring	2.02	0.962	3.363	0.0194	0.122	4.073	0.0173
Midspring	2.03	1.783	3.361	0.00309	0.671	4.918	0.00228
Late spring-early summer	2.02	1.892	5.938	0.0189	0.833	7.972	0.0141
Midsummer-late summer	2.03	1.615	1.730	0.0145	0.497	2.391	0.0105
Early autumn	2.10	1.471	0.652	0.00678	0.284	1.0952	0.00403
Midautumn	2.09	1.150	0.655	0.00615	0.256	0.748	0.00539
Late autumn (1977)	2.09	1.393	1.088	0.0119	0.310	1.2935	0.00997
Late autumn (1978)	2.15	1.492	0.767	0.00949	0.198	1.133	0.00676
Gulf of Maine							
Late winter-early spring	2.06	1.045	1.261	0.00630	0.041	1.685	0.00471
Midspring	2.03	1.571	2.037	0.00641	0.568	2.491	0.00524
Late spring-early summer	2.01	1.695	3.009	0.00772	0.796	3.508	0.00662
Midsummer	2.05	1.675	0.977	0.00470	0.836	1.851	0.00252
Late summer	2.12	1.396	1.738	0.00985	0.423	2.059	0.00832
Midautumn (1977)	2.07	1.708	1.446	0.0049	0.920	2.230	0.00317
Midautumn (1978)	2.16	1.501	0.232	0.00302	0.614	0.395	0.00177
Late autumn	2.01	1.592	2.552	0.0154	0.683	5.147	0.00766

slope and elevation from all other seasonal lines and had a high r value (Table 2). Since the occurrence of siphonophores in large numbers has been reported in our sampling areas (Sumner 1911; Rogers et al. 1978), this predictive equation should be useful for future occurrences of this phenomenon.

A coefficient of variation (cv) was calculated for each group of displacement volume and dry weight measures in order to compare the relative variability between the two indexes. As expected, both indexes were highly variable, with cv's averaging 54.3% (31.6-133.5%) and 65.4% (33.4-147.8%) for displacement volume and dry weight, respectively. Surprisingly, of the 36 data sets, 31 exhibited higher cv's for dry weight than for displacement volume. A two-tailed variance test was used to determine whether this difference was significant (Lewontin 1966) for the paired displacement volume-dry weight values. Only GOM late autumn (1977) displacement volumes had a significantly ($P<0.05$) lower cv than the corresponding dry weights. When all values were combined, however, and a single cv calculated for each index, displacement volumes were significantly ($P<0.05$) less variable. This was unexpected, because water retained interstitially and intracellularly should increase variability among displacement volumes. It appears, then, that displacement volume is a more consistent and more reliable measure of plankton standing stock than dry weight.

Zooplankton standing stock for 1977 and 1978 in each area is plotted in Figure 3A-C. The measures are juxtaposed in order to reveal whether any discrepancies exist between the two patterns. For SNE and GB the two indexes of abundance follow strikingly similar patterns. In the GOM, however, the dramatic midautumn increase in dry weight for 1977 is not equally reflected by the displacement volume curve. *Calanus finmarchicus* dominated these samples (Sherman et al. 1978) and further examination revealed that they were stage V copepodites, the condition in which they overwinter. Comita et al. (1966) showed that *C. finmarchicus* collected from the Bute Channel, England, reach their weight and caloric maxima in autumn and early winter, with stage V individuals having the highest values. The impact these overwintering preadults had on the dry weight measures was confirmed by plotting the seasonal mean dry weight-displacement volume ratios for all three areas (Fig. 4). GOM autumn ratios were highest for both years, 17.4% and 13.4%, respectively. Furthermore, samples dominated by *C. finmarchicus* had higher ratios than samples from shallower stations where the copepods *Pseudo-*

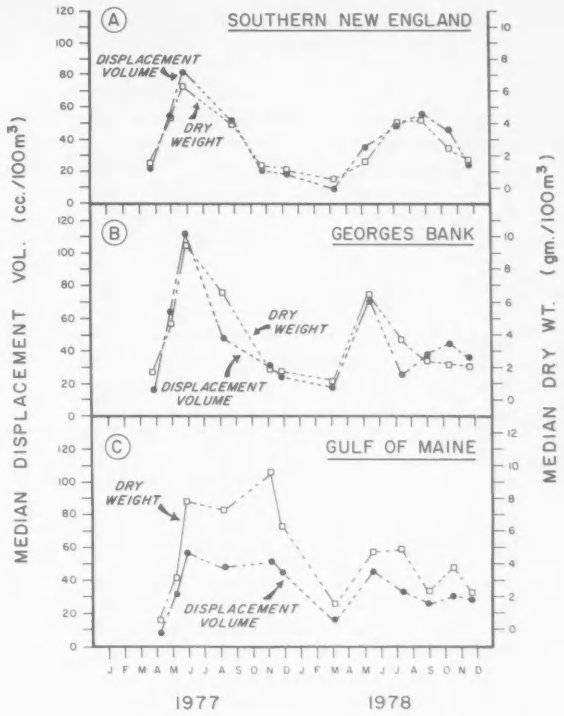

FIGURE 3.—Changes in median displacement volumes and dry weights for A) Southern New England, B) Georges Bank, and C) Gulf of Maine waters. Dashed lines represent intersurvey periods. Similar abundance trends are portrayed by both indexes, but discrepancies in magnitude between measures occur for Georges Bank summer samples and throughout the year in the Gulf of Maine. Displacement volumes are from Sherman et al. (1977, 1978).

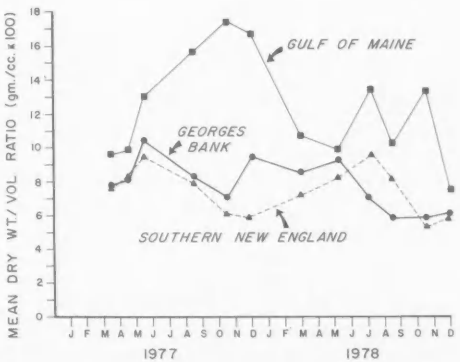

FIGURE 4.—Seasonal changes in dry weight/displacement volume ratios for the three sampling areas. Points are placed at the midpoints of the survey cruises. Gulf of Maine samples have higher values throughout the year.

calanus minutus or *Centropages typicus* were abundant. The preadult *Calanus* apparently store lipid reserves for survival through the winter and represent a substantial biomass underestimated by displacement volumes.

Autumn increases in dry weight were not observed for GB or SNE, though both areas support large populations of *Calanus* in the spring and summer. In general, overwintering *Calanus* remain in deep water and do not migrate vertically (Marshall and Orr 1955). The only concentrations of preadult *Calanus* found in these areas were at a few stations located near or below the 100 m contour line during late autumn. These samples had higher dry weight-displacement volume ratios than *Calanus* free stations. The GOM is able to support a large population of overwintering *Calanus* in deepwater basins.

Discussion

The linear relationship between displacement volume and dry weight is affected by the seasonal changes in species composition and age structure which occur throughout the year in zooplankton communities. Accurate interconversion between them is possible only with a ser-

ies of seasonal equations that are restricted to a specific area. A single general conversion equation derived from samples from a widespread area cannot provide estimates of abundance with sufficient accuracy to describe the variation in abundance and community composition necessary for detailed studies of trophic structure and community composition. The findings presented here are generally consistent with those of previous investigators (Lovegrove 1966; Platt et al. 1969; Beers 1974), with the exception of Wiebe et al. (1975). It should be recognized that the latter approach (Wiebe et al. 1975) has utility in comparing disparate data sets from different geographical areas and seasons. It is necessary to recognize the limitations of each approach and select according to the intended use of the data.

Previous reports have recommended dry weight determinations over displacement volumes because both interstitial and intracellular water is eliminated from the sample, removing bias caused by gelatinous organisms (Ahlstrom and Thrailkill 1963; Beers 1974). Further, since only organic and inorganic substances remain in the sample, dry weight should provide information regarding the potential food value of the plankton standing stock. However, the high correlation found between displacement volume and dry weight ($r = 0.925$, 442 df) implies that both measures provide equivalent assessments of standing stock and potential food value. In two of the three areas investigated, GB and SNE, both measures portray identical ascending and descending trends in biomass with maximal and minimal points closely correlated (Fig. 3). In addition, variability, though high for both techniques, is higher for dry weight.

Discrepancies between the two measures appear, however, when one examines GOM data. Standing stock is underestimated by displacement volume because samples there have high dry weight to displacement volume ratios (Fig. 4). As a consequence, when biomass is compared between the GOM and GB or SNE, each index gives a different interpretation of between-area differences (Fig. 5). For example, in autumn 1977, mean dry weight for the GOM was five times higher than for SNE, but mean displacement volume was only twice as high. This phenomenon is attributed to the life history of *C. finmarchicus* in the GOM. Dry weight values reported by other investigators from different areas are also more readily comparable than displacement volumes because Lovegrove's technique (1966) for measuring them has been widely accepted, while techniques for measuring displacement volumes vary, especially in the attempt to remove interstitial water (Wiebe et al. 1975). Thus, for studies comparing standing stock between different sea areas, and for other advantages previously mentioned, dry weight is the preferred measure.

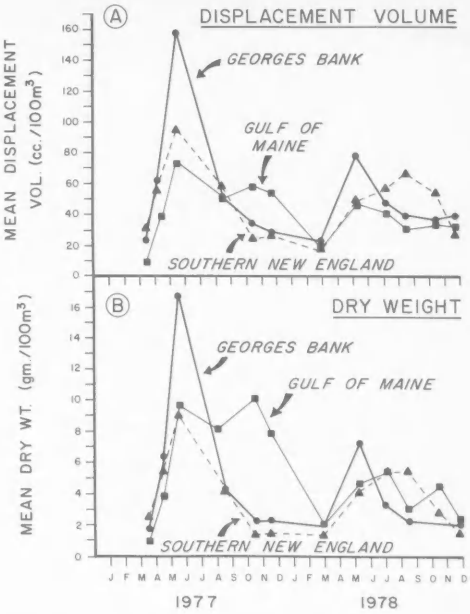

FIGURE 5.—Trends in plankton abundance for the three areas in 1977 and 1978 as measured by A) displacement volume, and B) dry weight. Each measure gives a different interpretation of between-area differences in biomass, especially in the Gulf of Maine.

Summary

This report has provided a series of season- and area-specific equations for the interconversion of zooplankton displacement volume and dry weight. In addition, interconversion equations for samples with large amounts of phytoplankton and siphonophore fragments have been calculated. However, dry weights should be measured directly on samples containing organisms with large amounts of intracellular water because they drastically affect the biomass rela-

tionship. It is our experience, however, that these organisms are abundant only on rare occasions in the MARMAP study area. The predictive equations should assist investigators assessing zooplankton standing stock on the continental shelf of the Northwest Atlantic.

General conversion factors at best yield only gross estimates, thus investigators should be aware of the limitations imposed by these values. A decision must be made by the investigator as to what level of accuracy is acceptable on the basis of what the data is to be used for. Further breakdown of the data into smaller subsets than area and season is possible, but the result would be an unwieldy number of equations sensitive to minute changes in trophic conditions. However, one can conclude from this study that effective displacement volume to dry weight conversion equations must to some extent take into account seasonal and areal variations in community composition. Given these considerations, the data presented here show no increase in variability inherent in displacement volume over dry weight biomass measures. Displacement volume provides a simple, easily routinized, rapid and nondestructive method of representing biomass, which is appropriate for processing the large numbers of samples typical of survey sampling programs.

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ESTIMATION OF EQUILIBRIUM SETTLEMENT RATES FOR BENTHIC MARINE INVERTEBRATES: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA: PELECYPODA)

It is generally agreed that marine invertebrates possessing planktotrophic larval stages experience extremely high mortality during the early stages of their life history. In the settlement of benthic invertebrates, mortality occurs during three critical phases: 1) fertilization, 2) the free-swimming pelagic stage, and 3) the early postlarval attachment period. Since egg loss, larval recruitment, and early postlarval mortality may often be the limiting steps in the development and maintenance of marine benthic communities, it is of interest to ecologists to be able to make direct estimates of settlement rates in such populations.

It is often difficult, however, to obtain reasonable estimates of early life history stage mortality rates. The earliest attempt to determine such rates was made by Thorson (1966). Based on the standing crop of a population of *Venus* (= *Mercenaria*) *mercenaria*, he estimated that approximately 98.6% of the clams died during the postlarval period (stage 3) and that loss prior to this was probably much heavier. More recently, Muus (1973), in a study of 11 species of bivalves in the Oresund, Denmark, found postlarval mortality rates (stage 3) of 67-100% for all species; whereas Gledhill (1980) calculated larval mortality rates (stage 2) of 99.38% and 99.99% for two populations of *Mya arenaria* in Gloucester, Mass. None of these estimates, however, take into account the heavy mortality that occurs during stage 1, thereby overlooking the substantial loss occurring during the fertilization process itself.

In an attempt to overcome the difficulty in estimating early survival parameters empirically, Vaughan and Saila (1976) developed an indirect method using the Leslie matrix for determining mortality rates during the first year of life for the Atlantic bluefin tuna, *Thunnus thynnus*, assuming an equilibrium population. By expanding their treatment, as suggested by Van Winkle et al. (1978), it is possible to divide age class 1 into particular stages, thereby making the model appropriate for cases dealing with animals possessing more complex life cycles (i.e., those which include egg, larvae, postlarval juveniles, etc.). In the case of benthic invertebrates with free-swimming larval stages, this method can be used to calculate mortality rates during settlement for any species population for which demographic parameters are available. Such theoretical estimates are of special interest for two reasons. First, the equilibrium settlement rate (r_s) value can be compared with field-determined estimates; second, the value may be useful in the prediction of future age structures in natural populations.

This paper describes the indirect method for estimating the settlement rate based on age-specific fecundity and survivorship rates and discusses its application to a commercially important species of bivalve, *Mya arenaria*.

Results

Leslie Matrix

Matrix methods for analyzing age-structured populations were developed by Leslie (1945,

1948) and subsequently used in numerous studies of human and animal populations. In the present setting, the Leslie matrix takes the form:

$$L(r_s) = \begin{bmatrix} a_1 & a_2 & a_3 \ldots a_{n-1} & a_n \\ r_s b_1 & 0 & 0 \ldots 0 & 0 \\ 0 & b_2 & 0 \ldots 0 & 0 \\ . & . & . & . \\ . & . & . & . \\ . & . & . & . \\ 0 & 0 & 0 & b_{n-1} \quad 0. \end{bmatrix}$$

Here, a_i is the number of female eggs produced annually by a female *Mya arenaria* in class i (age $i-1$ to i), and b_i is the probability of a clam in class $i-1$ surviving to class i for $i \geqq 2$. The survivorship from age-class 1 to age-class 2 (P_o in the notation of Vaughan and Saila (1976)) has been divided into two factors, r_s and b_1. The factor r_s is the settlement rate, or the probability that an egg will develop into a clam with a 2 mm shell length (0-2 mo of age); b_1 is the probability that a clam with a 2 mm shell length will survive the remainder of the year (about 10 mo).

The intrinsic growth rate is an increasing function of the settlement rate, r_s. Therefore, the equilibrium value, $r_{s_{eq}}$, $0 < r_{s_{eq}} < 1$, can be calculated for the population assuming steady state conditions. Since the values of a_i and b_i have been determined the *Mya arenaria* (Brousseau 1978a, b), $r_{s_{eq}}$ can be determined for this species. Similar calculations are described by Vaughan and Saila (1976) and Van Winkle et al. (1978).

Calculation of Equilibrium Settlement Rate and Stable Age Structure

Under conditions of the Perron-Frobenius Theorem, the population will reach an equilibrium state (starting with any initial reproducing population) if $\lambda = 1$ is the dominant eigenvalue of $L(r_s)$. Thus, $r_{s_{eq}}$ is the unique solution to the equation

$$|L(r_s) - \mathrm{I}| = 0.$$

By induction on the size of the matrix (n),

$$|L(r_s) - \mathrm{I}| = \pm (1 - a_1 - r_s b_1 a_2 - r_s b_1 b_2 a_3 - \ldots - r_s b_1 b_2 \ldots b_{n-1} a_n).$$

The required settlement rate is given by:

$$r_{s_{eq}} = \frac{1 - a_1}{b_1 a_2 + b_1 b_2 a_3 + \ldots + b_1 b_2 \ldots b_{n-1} a_n}.$$

Using the data in Table 1, the required settlement rate for *Mya arenaria* is $r_{s_{eq}} = 0.001462\%$ or 1 egg out of about 68,400 survive to 2 mm. Thus 1 egg out of 384,000 must survive the first year to maintain a steady population. Errors of up to 5% in the fecundity and survivorship values will yield equilibrium settlement rates of between 0.000983% (1 egg in 101,700 surviving to 2 mm size) and 0.00218% (1 egg in 45,800 surviving to 2 mm size). In addition, the eigenvector corresponding to the eigenvalue $\lambda = 1$ gives the stable age structure for the population. Postsettlement population structures were determined for only the $r_{s_{eq}}$ calculated above. The results are given in Table 2.

TABLE 1.—Life history statistics used in the derivation of the Leslie Matrix for *Mya arenaria*. (Data from Brousseau 1978b.)

Age (yr)	Age class	Shell length (mm)	Fecundity[1] (a_i)	Probability of survival (b_i)
0-1	1	2.0-29.9	0.0	0.177
1-2	2	30.0-44.9	3,744.0	0.912
2-3	3	45.0-59.9	17,170.0	0.904
3-4	4	60.0-64.9	31,159.0	0.952
4-5	5	65.0-69.9	39,957.0	0.949
5-6	6	70.0-74.9	50,341.0	0.969
6-7	7	75.0-79.9	62,460.0	0.984
7+	8+	80.0-84.9	76,465.0	0.911

[1]Fecundity = number of female eggs produced per individual, assuming a 1:1 sex ratio.

TABLE 2.—Calculated stable age structures for the population of *Mya arenaria*, based on the entire population and the adult population (≤30 mm) only.

Age class	Percent of entire population	Percent of adult population (≤30)
[1]1	42	
2	7	12
3	7	12
4	6	10
5	6	10
6	5	9
7	5	9
8	5	9
9	5	9
10	4	7
11	4	7
12	4	7

[1]This age class represents clams 2-29.9 mm in shell length.

Discussion

In his classic work on marine invertebrate communities, Thorson (1950) stated the definitive "number of eggs and larvae produced per pair of adult animals per lifetime to maintain the population is...one pair of larvae." More simply, to remain at equilibrium, a replacement rate of one must be maintained. For a population of *Mya*

arenaria possessing the life history statistics given above, 1 out of about 790,000 eggs produced during the lifetime of an individual must survive to ensure continuance of the population.

However, variable recruitment and high postlarval mortality tend to be the general rule among temperate and boreal marine invertebrates, especially the bivalves. At the Jones River in Gloucester, the tidal flat received a heavy set of young *Mya arenaria* in 1973 (Brousseau 1978a, b). Based on crude estimates of stock density, age-specific fecundity, and the density of the resultant spatfall, the settlement rate was 0.0498%, or about 34 times larger than the calculated $r_{s_{eq}}$. During the two subsequent years, on the other hand, this site received only a limited spatfall, which, coupled with high postlarval mortality, resulted in settlement rates of 0.0%. Under such fluctuating conditions, therefore, the settlement history of a population takes on added significance.

In addition to being of theoretical interest, determination of the equilibrium settlement rate for a commercially important species may be of value in its harvesting management as well. Although the impact of repeated exploitation is difficult to assess given the uncertainties of environmental conditions, continued harvesting on tidal flats receiving annual settlement rates below equilibrium may prove to be extremely harmful to the resident population.

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GROWTH OF JUVENILE RED SNAPPER *LUTJANUS CAMPECHANUS*, IN THE NORTHWESTERN GULF OF MEXICO[1]

The red snapper, *Lutjanus campechanus*, has received considerable attention in the past due to its importance as a commercial and sport fish in the Gulf of Mexico. Most published material deals with the fishery and is summarized in Carpenter (1965). Few major papers have dealt with the natural history of red snapper.

Moseley (1965) reported on growth, reproduction, and food habits of red snapper taken by trawl and handline off the Texas coast. He determined age and growth rate from scales by assuming that growth checks were produced during the spawning season. Bradley and Bryan (1975) also sampled red snapper along the middle Texas coast with trawl and hook and line. They were unable to distinguish age classes by length frequencies and attributed that to an extended spawning season. Futch and Bruger (1976) used otolith readings to determine age and growth of red snapper off the coast of Florida.

This paper presents new information on growth of young snapper and relates that information to their occurrence on an artificial reef.

[1]University of Texas Marine Science Contribution No. 519.

Study Area and Methods

The artificial reef, composed of three sunken World War II liberty ships, is located approximately 29 km offshore (lat. 27°35′N, long. 96°54′W) from Port Aransas, Tex., in 33 m of water. Red snapper were collected from the reef with fish traps in March, May, July, September, November, and December 1979. The rectangular traps (1.8m × 1.2m × 0.6m) were made of 1.25 cm reinforcing bar covered with 3.4 cm mesh plastic coated wire. The entrance cone had an initial opening of 60.9 × 45.7 cm terminating in a 90° downturn with a 25.4 cm diameter entrance port. During each sampling period, five traps were baited with fish scraps and set on the bottom around the reef for 24 h. All red snapper captured in traps were measured in standard and total lengths and placed in a flowing seawater live box onboard ship. Snapper which were in good condition after 1 h on board ship were tagged with numbered internal-anchor tags and released over the artificial reef.

Small red snappers (<160 mm) were collected from the south Texas outer continental shelf during 1975 through 1977 with a 10.7 m "flat trawl" with 4.45 cm stretch mesh in the body and 2.5 cm stretch mesh in the bag. From 1975 to June 1976 a 9.5 mm stretch mesh liner was used inside the bag. Trawl sampling depths ranged from 10 m to 132 m. Seventy-two trawl samples were taken in 1975, 222 in 1976, and 294 in 1977. All trawls were made at a speed of about 2 kn for 15 min. (For details of sampling sites and procedures see Flint 1981.)

Results

Growth

The smallest fish taken in the trawl samples were generally 20-29 mm (Table 1). Juveniles <40 mm were caught in August, September, and October, and eight individuals of this size were taken in June 1976. Two year classes can be identified in the length-frequency table (Table 1) and followed for 12-18 mo. The smallest fish taken in traps at the ship reef were 100-110 mm. Snapper <100 mm could escape through the mesh.

Length-frequency histograms for combined trawl and trap data are shown for each month (Fig. 1). Two cohorts, age group 0 and age group I, are apparent in the data and a third cohort, age group II, may be present in the March and July data.

Recruitment of small snapper (<40 mm) into the population occurred primarily in June and July as evidenced by the modal size of the age 0 year class in August, September, and October. Limited recruitment of small fish continued into October. Length-frequencies of snappers captured in June through December were distinctly bimodal. Modal size classes for age I fish were 110 mm in June and 130 mm in July. Modal size classes for age I+ fish were 150 mm in December

TABLE 1.—Length-frequency distribution of red snapper caught in trawl samples. The number of individuals of each size class in each month is shown. No samples were taken in months with an asterisk (*).

	1974	1975												1976											1977									
Length	D	J	F*	M*	A	M	J*	J*	A	S	O*	N*	D*	J*	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
10-19																			1																		
20-29									2	12									6																		
30-39									1	4									1			1	5														
40-49	1								7						1							3	12	6	1									2	3		
50-59	2								8	1						1						11	1	7	1	1								11	10		
60-69	5				1				3	1					11							1	3	3			1		1					24	11	1	
70-79	4				4				4	4					6							4	7							8				26	20	1	1
80-89	1	1			1	1			1	3					3				1			13	3	3				1		5				27	16	2	
90-99	2					2									6	2	2		2			9	4		1				2	4				5	2		
100-109	1															2			2			1					1			4				2	2	1	
110-119						1									2				2											5	2					1	1
120-129	1														1				1											3							
130-139	1														3				1																		
140-149																					1	2													1		
150-159																1						1												1			
160-169																				1	1						1										
170-179																				3		1					2	1							2		
180-189																												3									
190-199																						1						5									
200-209																					1							3									
210-219																												1									
220-229																												2									
230-239																												1									

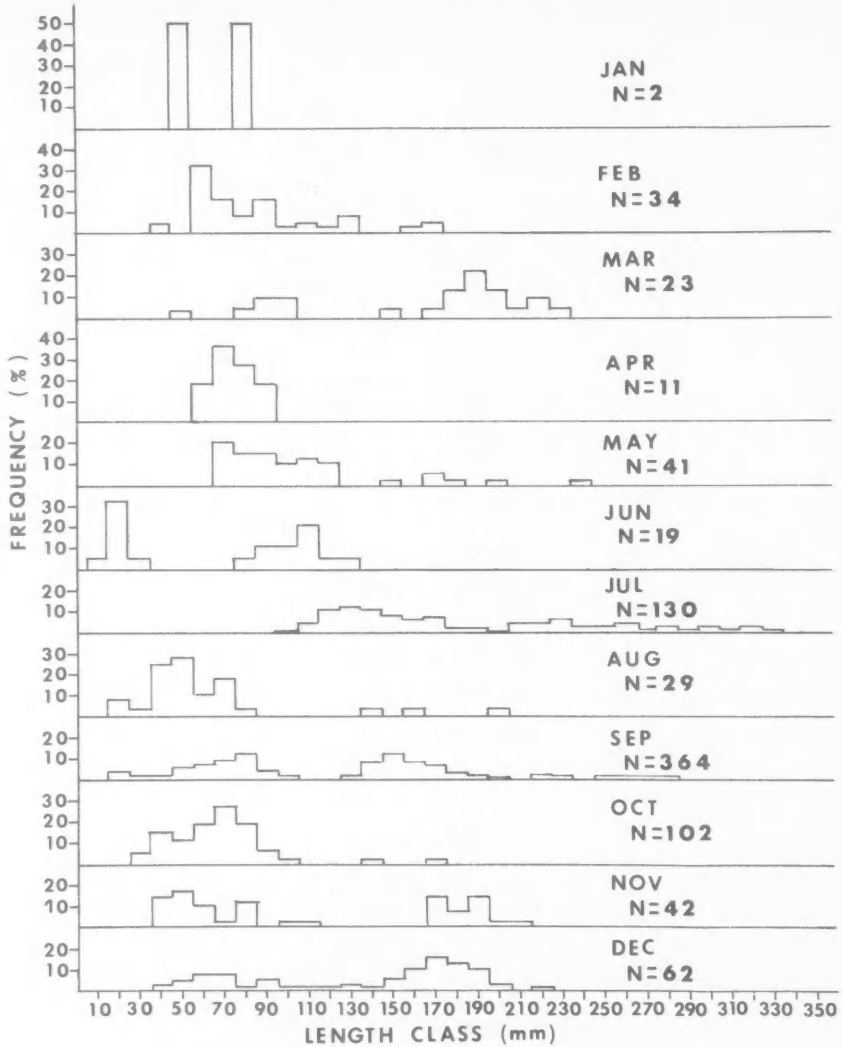

FIGURE 1.—Size distribution of young red snapper from pooled trawl and fish trap collections.

and 190 mm in March. It appears that age II snapper were 210-230 mm in July although few fish of that age class were caught.

Tagging

Numbered, internal-anchor tags were placed in 267 red snapper between 117 and 350 mm (mean = 192 mm) on the ship reef in July, September, and November 1979. Sportfishermen returned 28 tags and our fish trap sampling produced seven additional returns (13% total return rate). All fish were recaptured from the ship reef. The longest "free time" for any fish in our study was 92 d except for one fish which was tagged and recaptured twice over a 112-d period.

Sixty-three percent of the recaptures were within 30 d of release. No fish were recaptured after 11 December 1979 despite continued fishing effort on the ship reef during the winter and spring of 1980.

Measurements from the seven fish recaptured by our own sampling yielded growth rates of 0.12-0.55 mm/d (mean = 0.29 mm/d). Based on age determination from our length-frequency plots, these represent growth rates of age I+ snapper. Lengths of recaptured red snapper reported by sportfishermen were not considered accurate enough to use for growth determinations.

Discussion

Bimodal size distributions of red snapper caught in trawls and traps indicate that juvenile red snapper grow more slowly than previously thought. Moseley (1966) presented the first detailed account of growth rates for snapper using scale annuli for age determination. He assumed that growth checks were produced during the spawning period rather than during a midwinter slow growth period, an assumption confirmed by later workers (Futch and Bruger 1976). Moseley (1966) found that fish with one spawning check averaged 250 mm and determined a growth rate of about 90 mm between spawnings (about 0.25 mm/d). He proposed that red snapper grow 200-230 mm during their first year. Bradley and Bryan (1975) cited other unpublished data from Texas which indicated an initial growth check on scales at about 200 mm fork length and a mean growth rate of 60 mm/yr between formation of the first and the fifth rings. Futch and Bruger (1976) determined that maturity is probably reached after the second year (age II+) in Florida. Their data also indicated that the first growth check (on otoliths) generally occurred on snapper of about 200 mm.

A slower growth rate could be inferred from otolith, scale, and vertebrae aging by Bortone and Hollingsworth (1980) who found that snapper with one growth check averaged 163 mm and snapper with two growth checks averaged 197 mm. Small sample size (46) and one sampling date (17 October) may have influenced their results. That snapper mature at age II+ (Futch and Bruger 1976) and produce growth checks as a result of spawning activity suggest that fish with a single annulus are not age I+ as Moseley (1966) suggested but are age II+. Our data are consistent with this hypothesis. The distinct bimodality in length frequencies of snapper <220 mm during June through December (Fig. 1) indicates the presence of two year classes within this size range. We propose that red snapper grow to 110-130 mm during the first year and attain a size of 220-230 mm the second year. It is at this size (age II) that they apparently reach sexual maturity (Camber 1955; Futch and Bruger 1976). This growth rate is consistent with established postspawning growth rates of 60 (Bradley and Bryan 1975) to 90 mm/yr (Moseley 1966) between the first and fourth or fifth spawnings.

Red snapper >160 mm were uncommon in our trawl samples. Bradley and Bryan (1975) also collected few snapper between 150 mm and 220 mm in trawl or hook and line catches. Numerous fish of this size were trapped at the ship reef in July and September. Tagging data indicated that 130-250 mm (age I and early age II) snapper were abundant on the ship reef from July through September and some remained there through November or December. The absence of tag returns after December indicates that the fish present there all summer and fall either moved away, presumably to deeper water (Moseley 1966; Bradley and Bryan 1976) or had suffered substantial mortality. Fable (1980) found essentially no movement in 17 returns from 299 tagged red snapper in 60 m of water off the Texas coast.

Conclusions

1. We suggest that growth rates of juvenile red snapper during the first 2 yr are slower than previously reported. Our data indicate snapper attain a length of 110-130 mm the first year and 200-230 mm the second year.
2. Juvenile snapper <150 mm were common in trawl samples throughout most of the year.
3. Snapper 130-250 mm were common on the artificial reef from July through December. Tagging studies indicated the snapper remain around the artificial reef during the summer and fall but none were captured there or elsewhere after December.

Acknowledgments

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AN ASSOCIATION BETWEEN A PELAGIC OCTOPOD, *ARGONAUTA* SP. LINNAEUS 1758, AND AGGREGATE SALPS

Biologists working in the epipelagic zone of the ocean have reported that representatives of numerous planktonic taxa seem to be closely associated with gelatinous zooplankton, including hyperiid amphipods (Madin and Harbison 1977; Harbison et al. 1977; Laval 1980), gammarid amphipods (Vader 1972), isopods (Barham and Pickwell 1969), decapods (Shojima 1963; Thomas 1963; Trott 1972; Bruce 1972; Herrnkind et al. 1976), cyclopoid copepods (Heron 1973), mysids (Băcescu 1973), cirripedes (Fernando and Ramamoorthi 1974), and fish (Mansueti 1963; Janssen and Harbison in press).

Some symbionts in these groups are morphologically adapted to feed principally on the host and/or on the food material which the host collects, while others seem to associate more intermittently with gelatinous zooplankton, dependent on their nutritional state and that of the gelatinous hosts. Accordingly, symbioses may range from specific, structural associations to temporary or casual associations.

In this note we report a previously undescribed association between a cephalopod and a planktonic gelatinous herbivore. While conducting research scuba studies of gelatinous zooplankton in the western Gulf of Mexico, we collected juvenile pelagic octopods of the genus *Argonauta* sp. Linnaeus 1758, in association with aggregate generation salps (*Pegea socia* (Bosc 1802)).

The salp chains were composed of 40-60 individuals, each approximately 10 cm in apical/basal length. Individuals within the aggregate generation of *Pegea socia* (Bosc 1802) are uniformly covered with fine reticulated gold pigmentation and contain orange nucleii. The individuals each have four noticeable body muscles forming two x-shaped groups. Within each group, the pair of muscles are not fused dorsally. Endostyle bands of each individual are slightly arched.

Two juvenile octopods, a male and female with mantle lengths 8.4 mm and 6.7 mm, respectively, were collected from separate chains at a depth of 5-10 m at lat. 26°21′N, long. 95°45′W, on 26 February 1981. The males and females of *Argonauta* sp. have eight circumoral appendages, none of which are filiform. The body is not flattened, has no fins and no aquiferous pores on the head. The dorsal arms of the female are not

connected by a deep web and have broad terminal expansions modified for secretion of an external shell of egg case when mature. The left third arm of the male is hectocotylized, autonomous, and coiled up in a sac beneath the left eye.

The octopods were first noted inside the branchial cavity of one of the aggregate salps, attached by their tentacles to that individual's pharynx wall; however, they both left their hosts during our capture of the salps in quart jars. We found only one octopod per salp chain, though the salps had many hyperiid amphipods (*Vibilia armata* Bovallius 1887), cyclopoid copepods (*Sappharina angusta* Dana 1852), and fish in association. We found no morphological damage to the individual aggregate salps which had hosted the octopods.

The association of juvenile octopods with salp aggregates may afford a source of food (commensal amphipods), flotation, transportation, and/or camouflage to the octopods. Examination of Formalin[1]-preserved gut contents from these octopods was inconclusive, however, since neither octopod had fed recently and only unidentifiable, residual solids remained in the gut. It is improbable that the octopod was seeking protection by attaching to the salp chain, since moving out from the host was an immediate reaction to in situ visual stimuli and/or local perturbations.

We thank C. E. Lea and G. J. Denoux for their identification of the octopods and copepods, respectively. Identification of the octopods was based on generic characteristics described by Voss (1956). Salps were classified as *Pegea socia* (Bosc 1802) as described by Madin and Harbison (1978). Amphipod identification was based on body shape, eye structure, and character of pereiopods as described by Bowman and Gruner (1973) for genus and Dick (1970) for species. Copepods were identified by body shape, segmentation, and appendage characteristics as described by Owre and Foyo (1967). Research scuba operations were supported by the National Science Foundation, grant OCE78-22481.

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[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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MIGRATION OF A JUVENILE WOLF EEL, *ANARRHICHTHYS OCELLATUS*, FROM PORT HARDY, BRITISH COLUMBIA, TO WILLAPA BAY, WASHINGTON

Juvenile wolf eels, *Anarrhichthys ocellatus*, were rarely reported off the Washington-Oregon coast prior to 1979. One 87 mm juvenile was collected by midwater trawl in 1962, 80 km off Newport, Oreg. (Wakefield 1980[1]). Another juvenile of 468 mm standard length (SL) was caught in 1969 (51 sets) by personnel of the Northwest and Alaska Fisheries Center, National Marine Fisheries Service (NMFS), while purse seining for juvenile salmonids in shallow marine waters (<30 m in depth) adjacent to the mouth of the Columbia River.

While purse seining for juvenile salmonids in these same waters, no wolf eels were caught in either 1978 (49 sets) or 1980 (67 sets) by NMFS, but in 1979 (109 sets), 19 specimens between 467 and 531 mm SL were collected. Oregon State University (OSU) personnel caught 113 juveniles during a 10-d purse seine cruise for juvenile salmonids in 1979 (56 sets) between the Columbia River and Coos Bay, Oreg., in waters >30 m. These fish ranged in size from 281 to 610 mm SL (Wakefield 1980). The purse seine used in waters <30 m deep fished to a depth of about 6 m (verified by the author using scuba). Based on its construction, the purse seine used in waters >30 m by both NMFS and OSU was assumed to fish to about 24 m deep.[2]

Personnel of NMFS, fishing in waters >30 m, collected seven juvenile wolf eels in 1980 (232 sets) between Copalis Head, Wash., and Tillamook Bay, Oreg. These fish ranged in length from 430 to 506 mm SL.

One of these juvenile wolf eels had been tagged on 24 October 1978 off Doyle Island near Port Hardy, British Columbia (Fig. 1), by personnel of the Canadian Department of Fisheries and Oceans (Bailey[3]). The tag was applied incidentally to a purse seine tagging operation for chum

[1]Wakefield, W. W. 1980. Occurrence and food habits of pelagic *Anarrhichthys ocellatus* juveniles collected off the Oregon coast during June, 1979. Paper presented at Sixtieth Annual Meeting of the American Society of Ichthyologists and Herpetologists at Texas Christian University, Fort Worth, Texas, June 15-20, 1980.

[2]J. Jurkovitch, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, pers. commun. February 1981.

[3]D. D. Bailey, Chief, Salmon Services, Department of Fisheries and Oceans-Pacific Region, 1090 West Pender St., Vancouver, British Columbia V6E 2P1, pers. commun. August 1980.

FIGURE 1.—Location of tagging (Port Hardy, B.C.) and recapture (Willapa Bay, Wash.) sites of a juvenile wolf eel.

salmon, *Oncorhynchus keta*. Only one wolf eel was tagged and its length was not recorded (Gould[4]). The juvenile was recaptured on 12 July 1980, 23 km off Willapa Bay, Wash., and was 502 mm long (Fig. 1). Distance traveled from tagging location to recapture site was about 593 km in 628 d. Approximate average movement was 0.94 km/d.

Information about the early life history of wolf eels has been sparse. Kanazawa (1952) and Marliave (1978) both observed a change to adult characteristics of pigmentation and dentition at lengths between 500 and 600 mm SL. Marliave, who has reared wolf eels at the Vancouver Public Aquarium in British Columbia, placed the juvenile-adult changeover at the end of the first year of life. He also noted that the fish, by the age of 3 mo, had begun to prefer the bottom except when feeding. Shelter seeking and territoriality became evident between 4 and 5 mo of age and about 200-400 mm long. At the end of 15 mo the fish ranged from 600 to 950 mm in length with a mean of just under 700 mm.

The tagged juvenile specimen has provided the first evidence of a difference in early life history of wild wolf eels compared with aquarium-reared fish with regard to juvenile behavior, growth rate, and length of time in the juvenile phase. This wolf eel possessed juvenile characteristics of coloration and dentition and was a minimum of 2+ yr in age. It was pelagic and below the lower end of the growth range attained by aquarium fish in 15 mo.

There have been no reports in the literature documenting migratory behavior of this species. Adult wolf eels are known to exhibit strong territoriality and attraction to some type of structure as shelter. Also a strong homing instinct exists even though a considerable amount of territory is covered while feeding away from shelter (Hulberg and Graber 1980).

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MARLIAVE, J. G.
1978. Laboratory culture of wolf eels. Annu. Proc. Am. Assoc. Zool. Parks Aquar., p. 160-167.

[4]A. Gould, Biologist, South Coast Division, Department of Fisheries and Oceans-Pacific Region, 1090 West Pender St., Vancouver, British Columbia V6E 2P1, pers. commun. December 1980.

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